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COMPARATIVE ANATOMY OF THE LUNGS

by

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FOREWORD

In the preparation of this thesis on The Comparative Anatomy of the Lungs it was found that some knowledge of the natural history of the animals discussed was helpful in understanding the lung structure and adaptations for respiration. For this reason, a very limited amount of natural history is included.

The system of giving credit for the references is as follows: if all the ideas in a paragraph were taken from one article, the reference is listed after the close of the paragraph; if credit is given for one sentence, the reference is included in the sentence; if only one article on the topic was available, as was often the case, credit is given in a footnote.

COMPARATIVE ANATOMY OF THE LUNGS

INTRODUCTION

Need for oxygen

All forms of animal life require some means of securing oxygen and removing carbon dioxide. This process is called respiration and includes an external aspect or breathing, concerned with the gaseous exchange of oxygen and carbon dioxide between the blood and the water or air; and an internal aspect concerned with the transfer of these gases between the blood and the cells of the body. The latter is the effective part of respiration that results in the oxidation of organic material, releasing heat and energy.

The respiratory organs perform these functions and to do so efficiently they must have the following essentials. (1) A great area of thin richly vascular tissue exposed to the oxygen-containing medium, water or air. This area must be extensive enough and sufficiently permeable to insure adequate osmosis of gases for the organism concerned. (2) The tissue must be kept moist in order to allow for thinness and permeability without drying on exposure to the air. (3) There must be an adequate mechanism for frequently changing the water or air that is in contact with the respiratory surfaces, as neither the oxygen nor the carbon dioxide of metabolism can be stored within the body.

How needs are met

These conditions are met in a variety of ways by different animals. In simple forms there is no specialized respiratory apparatus, simply a diffusion of oxygen through the skin into the circulatory fluid and of carbon dioxide outward. In insects there is a system of thin-walled tubes, tracheae, that begin exteriorly in openings called spiracles and internally branch abundantly, carrying oxygen through the body to the cells.

Such methods as these are sufficient only for relatively small and simple animal forms. In vertebrates, where the bodies are comparatively large and the covering rather impervious a specialized apparatus for respiration developed. Most commonly the respiratory organs take the form of local outgrowths called gills or branchiae, adapted for aquatic respiration, or local ingrowths of bags of folded membrane called lungs, fitted for breathing air. A less common condition is the use of the anterior or posterior ends of the alimentary canal for respiration, and the use of the air-sac or swim-bladder in certain fishes as an accessory organ of respiration.

Development of the respiratory system in vertebrates

Adams (1933) traces the development of the respiratory system as it became specialized to meet the needs of the more complex vertebrate structure. The mouth and throat region could

do the respiratory work with the least modification since they are located at the beginning of the digestive tube in close contact with the water. Originally, perhaps the entire digestive tube shared in the respiratory function as suggested by the rectal breathing of certain modern fishes. The gills with their filaments or lamellae give the greatest exposure to the water, and the gill pouches and slits further increase the efficiency by permitting a steady stream of water to pass through them. The water passes in through the mouth to the pharynx, over the gills and out under the operculum which protects the gills. Capillaries in the gills bring the blood near the water so that exchange of gases is made easy.

The branchial system is found in all fishes and in some amphibians. Any animal entirely dependent on gills dies when changes in the water destroy the supply of oxygen. Therefore another method developed in fish that live under adverse conditions during part of the year. This began with modifications in the air-sac or swim-bladder, a structure present in fishes above the sharks. One of the many functions attributed to it is that of an accessory organ of respiration, and in this capacity it is used today by lung-fishes and a few others.

In all land and water tetrapods the lung is present with the exception of the lungless salamanders, in which the lung has been lost. These amphibians, living in swift mountain streams, carry on their respiration by capillaries in the walls of the

pharynx and anus, and through the skin. Very few tetrapods have lost the lungs.

Both gills and lungs may develop in the same individual but are usually not functional at the same time.

With the development of lung-breathing, the gill slits tended to close, sometimes remaining open in amphibians, but always closed in higher animals which develop special breathing passages through the throat and nose.

AIR-BLADDERS

General structure

The air-bladder is found in all fishes except the sharks and a few bottom living forms (Norman, 1931). It performs a variety of functions but only its relation to air-breathing is to be considered here.

Although the exact point of origin varies, the air-bladder is derived in most cases from the dorsal wall of the anterior end of the digestive tube and shows the same three layers histologically (Walter, 1928). It is located on the dorsal side of the body cavity above the peritoneum, so the latter covers it on the ventral side only. It is between the vertebral column, aorta, and kidneys on the dorsal side, and the alimentary canal on the ventral side. The length varies and often it extends from one end of the body cavity to the other (Kingsley, 1921). The walls are composed of connective, elastic, and muscular tissue. Internally, the surface may be smooth or spongy.

As the air-bladder increases in size, it remains connected to the gullet by only a narrow tube known as the pneumatic duct and corresponding to the trachea in higher animals (Norman, 1931). Fishes are classed as physostomi if the pneumatic duct remains open throughout life, and physoclisti if it closes or disappears giving the bladder the form of a closed sac. Dipnoi belong to the former group (Walter, 1928).

Some fishes with a pneumatic duct can fill the bladder by swallowing air, and these come to the surface to gulp the air. As a rule, however, the gas which entered the blood in the gills is secreted from the blood in the anterior part of the swim-bladder in the physostomous fishes and in the anterior chamber in physoclistous fishes.

Goodrich (1930) makes the following distinction regarding the secreting area. "The more primitive structure found in physostomous fishes, in which the gland is covered with a simple flat epithelium has, together with its rete mirabile, been named the red body, while the higher type found in physoclistous fishes, in which the gland is covered with thick glandular epithelium thrown into folds or sunk in crypts is named the red gland."

The "red gland" or "red body" produces free oxygen (O_2) by the breaking down of red corpuscles (Walter, 1928). This oxygen constitutes a large part of the gas that distends the swim-bladder. In river fishes it is said (Jordan, 1905) to be mostly nitrogen; in marine fishes mostly oxygen; in deep sea fishes oxygen greatly in excess.

The oxygen above what the fish requires escapes through the pneumatic duct in all physostomous fishes. In physoclistous fishes, the posterior chamber of the swim-bladder is lined with a capillary network, the rete mirabile, through which the excess gas is absorbed directly into the blood for removal by the gills. (Walter, 1928).

Specialized Air-bladders

A limited number of primitive fishes use the air-sac for respiration. They include the Crossopterygii, whose only living representative is Polypterus; Dipnoi represented by Ceratodus, Lepidosiren, and Protopterus; Ganoidia represented by Amia and Lepidosteus.

In all these the air-sacs are to some extent divided into alveoli, lined with blood vessels, and the pneumatic duct well developed, freely admitting air. In most fishes the duct opens into the esophagus from the dorsal side but in primitive forms, except Ganoids, it enters from the ventral side like the windpipe of the higher vertebrates. The common types of air-bladders are illustrated in Fig. 1. Between the undivided air-bladders of Amia and Lepidosteus and the completely divided air-bladder of Polypterus there are many degrees of bifurcation in the series of fishes.

Ganoidia

Lepidosteus or American Garpike (Fig. 2). The air-bladder is single and extends the entire length of the body cavity. The anterior end connects dorsally by a glottis with a vestibule that leads to the mouth (Fig. 3). Internally the lung is divided in halves by a fibrous band located along the median inner surface of the dorsal wall, from which extends ventrally a series of transverse fibro-muscular ridges that form the boundaries of a

double row of alveoli or recesses (Fig. 4). The bottom of each alveolus is further subdivided thus increasing the respiratory surface. (Cam. Nat. Hist. Vol. 7).

The air-bladder is probably a means of securing additional oxygen while the gills accomplish most of the elimination of carbon dioxide. Analysis of gases in the air-bladder shows that carbon dioxide rarely exceeds two per cent.

Amia (American bow-fin or mudfish.* The air-bladder is very large and extends the entire length of the body cavity. It is a median sac and is unpaired except that a short median cleft divides it in front into two short caeca, between which is the large duct communicating dorsally with the esophagus.

On each side there is a sheet of striated muscle consisting of two layers crossing each other like the internal and external oblique muscles of the abdomen of mammals. This muscle sheath serves to compress the air-bladder. No arrangement for its expansion has been detected and the experiments indicate that air is forced backward from the mouth into the air-duct by movements of the jaw, hyoid apparatus, and sides of the mouth.

The cavity of the air-bladder is so much divided that it can be compared with the lungs of reptiles, since it is more lung-like than lungs of salamanders and frogs. Its cellular network is well vascularized.

Experiments by Wilder show that Amia occasionally exhales bubbles of air and strongly indicate that each exhalation is

*From Wilder (1876)

followed by inhalation. These acts of aerial respiration are more frequent when the water is foul. Amia will live longer out of water than any other fish of American waters, longer even than the horned pout or mud minnow.

Crossopterygii

Polypterus (Fig. 5), the only living representative of the Crossopterygii, lives in sluggish waters and remains near the muddy bottom. If the water is foul it rises to the surface to gulp air, a part of which escapes through the gill openings.

Kerr (1910) brings out the following points about Polypterus. (1) The lung shows asymmetrical arrangement (Fig.6). The posterior half of the longer right lung is median in position. It is only in the anterior half where it is balanced by the shorter left lung that it bends toward the right. (2) Correlated with the increased size of the right lung, the left vagus nerve takes part in its innervation, the main branch passing across to the right lung dorsal to the esophagus. (3) The ventral glottis is not symmetrical in the adult in relation to the two lungs. It has undergone a shifting toward the right side and is in line with the larger right lung.

Point one (above) is a forerunner of the condition found in Dipnoi where the dorsal lung communicates with a ventral glottis around the right side of the alimentary canal. Point two explains the peculiar crossing of the nerves in the lung of the

lung-fishes where the pulmonary branch of the left vagus nerve extends on to the actually right lung by a path which is dorsal to the esophagus (Kerr, 1910).

Near the anterior end the two lobes fuse into a single chamber beyond which they project in the form of two short caeca. Internally there is no division into alveoli.

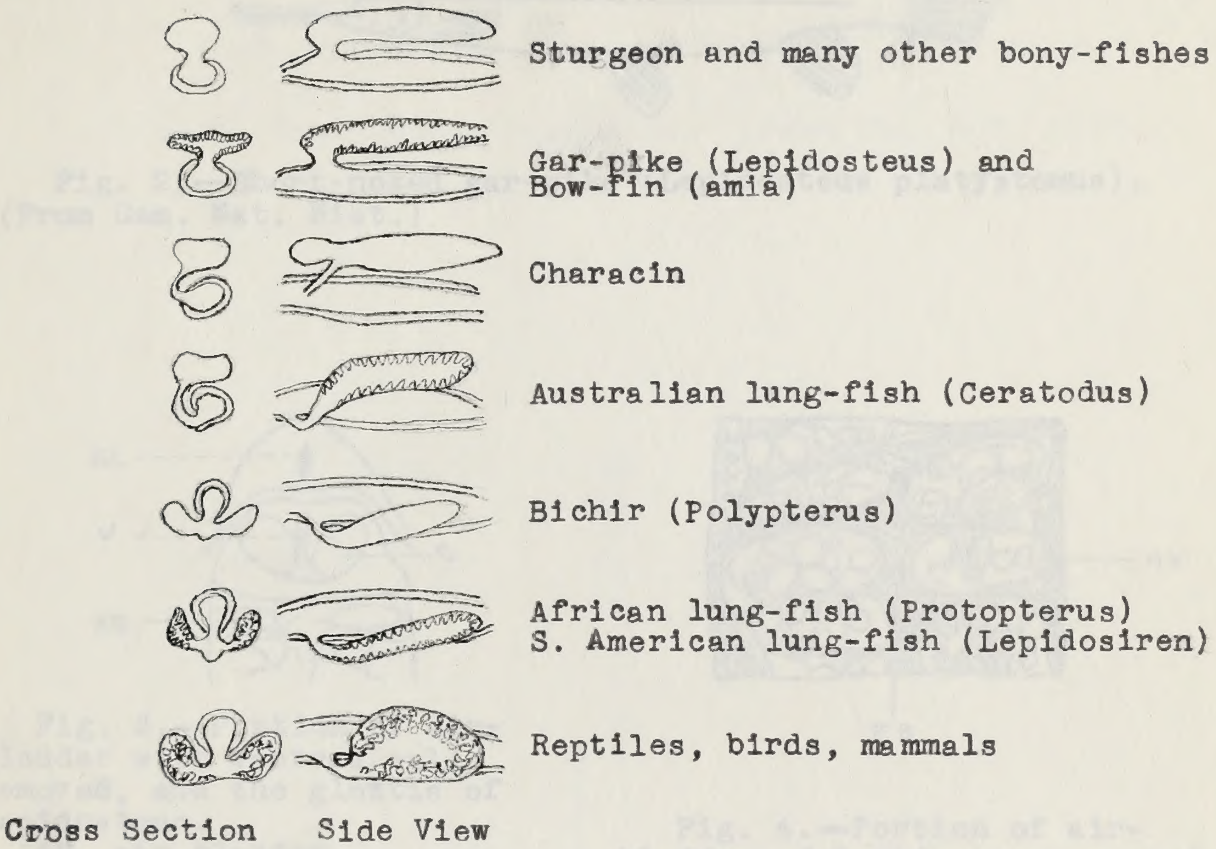

Sturgeon and many other bony-fishes
Gar-pike (Lepidosteus) and Bow-fin (amia)
Characin
Australian lung-fish (Ceratodus)
Bichir (Polypterus)
African lung-fish (Protopterus)
S. American lung-fish (Lepidosiren)
Reptiles, birds, mammals
Cross Section
Side View

Fig. 1.—Diagrams showing relation of air-bladder or lung to gullet in different fishes. (From Norman.)

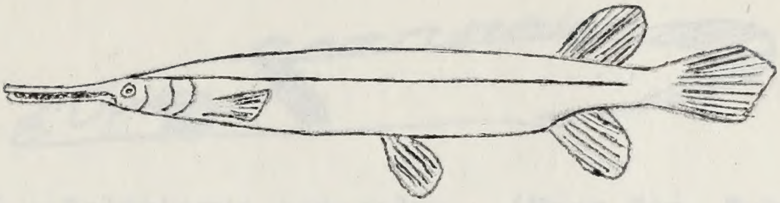


Fig. 2.—Short-nosed gar-pike (Lepidosteus platystomus). (From Cam. Nat. Hist.)

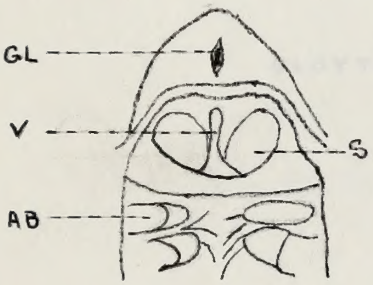


Fig. 3.—Portion of air-bladder with ventral wall removed, and the glottis of Lepidosteus.

AB, air-bladder
GL, glottis
S, bulging of hinder wall of vestibule into cavity of air-bladder
V, cleft leading from air-bladder into vestibule

(From Wiedersheim.)

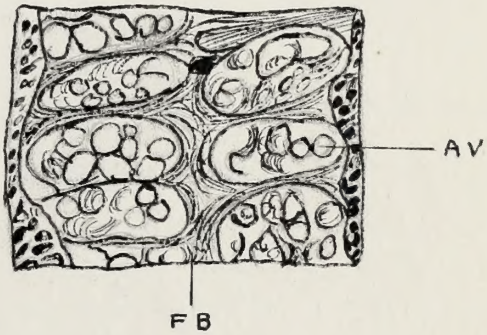


Fig. 4.—Portion of air-bladder of Lepidosteus, opened along mid-ventral line to show alveoli.

AV, alveolus
FB, medio-dorsal fibro-muscular band

(From Cam. Nat. Hist.)

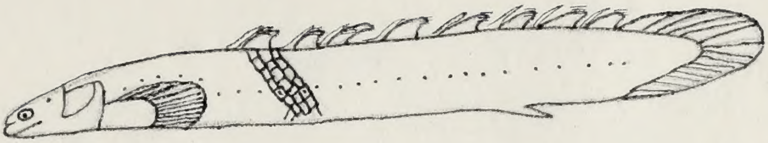


Fig. 5.—Polypterus senegalus. (From Cam. Nat. Hist.)

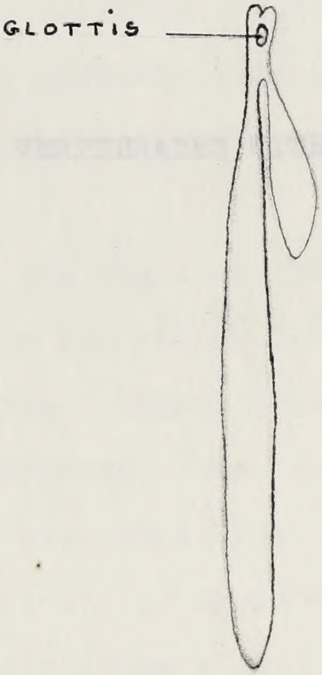


Fig. 6.—Air-bladder of Polypterus. (From Wiedersheim.)

VERTEBRATES WITH LUNGS

PISCES

Dipnoi (Lung-fishes)

Life and habits. The transition from air-bladder to true lungs which to some extent is indicated in Polypterus, Amia, and Lepidosteus, is more marked in the Dipnoi (Cam. Nat. Hist. Vol. 7) of which there are only three living genera (Fig. 7). Lung-fish are called primitive fish, a term that refers to their form, their internal characteristics, their lack of specialization in some respects and remarkable specialization in others (Coates, 1937).

A knowledge of the characteristics and habits of the lung-fish helps to explain the reason for structural modifications in the respiratory system. Dipnoi possess both gills and lungs, and are apparently between fishes and amphibians in classification. They possess structural features not found in other fishes but characteristic of amphibians, of which an air-bladder that functions definitely as a lung is of interest here.

Lung-fish live in tropical regions where the streams generally dry in summer and the fish remain inactive until the rainy season. During the period of aestivation the gills are not used for respiration, but instead, the pulmonary arteries bring impure blood to the air-bladder which then functions as a

lung, although both bronchi and trachea are absent.

When water is available it is often stagnant and impure. The fish occasionally come to the surface to change the air in the lungs. This enables them to exist in water unfit for fish that breathe entirely with gills. If the medium in which the fish happens to be is definitely unfit for breathing, the gills cease to function; if only to a less degree the gills may continue to assist in respiration.

In one of the few recent articles on lung-fishes, Coates (1937) says they are being studied at the present time in schools of medicine because "during long periods of aestivation they consume muscle tissue instead of fat, as in most animals; produce melanomas or colored cancerous growths;...permit concentration of urea in the blood in quantities 500 times greater than would be poisonous for most other vertebrates."

Ceratodus

Ceratodus or Neoceratodus as the modern form is called is the Australian lung-fish whose discovery does not date back further than 1870 (Gunther, 1871). This single species is restricted to a small area in Queensland, where it is rigorously protected by the government, and its capture and export forbidden, so it is not likely to be exhibited or available for study. This may explain the fact that no recent accounts are available, and older records are based on examination often of a single specimen.

Gunther (1871) gives the most complete account of both the habits and structure of Ceratodus. The animal lives in deep pools that retain a fair supply of water even in summer. Therefore Ceratodus makes no cocoon during the season of drought. It is helpless out of the water because its weak limbs which serve as paddles are not capable of sustaining the weight of the body or assisting in movement on land.

Lung structure in Ceratodus

The lung is a single sac extending from one end of the body cavity to the other. It occupies the middle of the dorsal region, being firmly attached to and along each side of the aorta.

Externally (Fig. 8) the surface shows rounded prominences corresponding to the internal chambers. Along the middle of both the dorsal and ventral surfaces is a stripe of fibrous tissue. Ventrally, the attachment between the lung and the intestine is firmest along this stripe.

The pneumatic duct is short and opens into the pharynx by a glottis on the ventral side, a little to the right of the median line (Cam. Nat. Hist. Vol. 7).

On the inner surface (Fig. 9) the fibrous stripes project slightly into the cavity of the lung. Between them extend a number of transverse septa forming the boundaries of a series of bilaterally symmetrical oval compartments or alveoli which

open toward the median line of the lung (Cam. Nat. Hist. Vol. 7). There are 28 on the left side and 33 on the right side, the latter extending further forward. The walls of the alveoli are still further divided by a network of fine ridges into smaller chambers.

Ceratodus has the best developed branchial system among Dipnoans and therefore the simplest lung. It can breathe either by gills or lungs alone or by both simultaneously.

Lepidosirenidae

Family Lepidosirenidae includes both Lepidosiren and Protopterus. The latter is found in the marshes of central Africa. During the dry season it burrows about 18 inches into the mud where a cocoon of slime is secreted, and here it remains inactive, connected with the surface by a small tunnel through which it breathes air with its lungs, and remains until the rainy season comes again.

Lepidosiren lives in marshes and swamps of South America. Like the African lung-fish it aestivates in the mud during the dry season. It is frequently brought to New York by animal and fish dealers from the equatorial belt of Brazil. In the hardened mud cocoon that encases it during the dry season it is easily dug out of the stream bed and packed for transportation. When placed in tepid water, the cocoon dissolves and the fish shortly revives.

In the New York Aquarium the South American lung-fish, under proper conditions will form a cocoon and in this state can be kept indefinitely, available for research workers (Coates, 1937). The breathing hole is about the diameter of a pencil at the surface, but half an inch below, the tube broadens to the thickness of the fish's body or even wider. It runs straight down for a few inches, and then ends in a sac-like cavity containing the singly looped body of the fish. From examination of the burrows, it appears that the lung-fish does not settle down quietly to complete aestivation until all possibility of remaining active is prevented by the hardening of the mud, but repeatedly comes as near to the surface to breathe as the mud permits. Its position in the burrow is always exactly the same, head pointed upward, body looped, and the thin tail covering the eyes to protect them.

A thin film absolutely impervious to water is secreted to prevent evaporation. It covers every bit of the body, and around the mouth turns inward for a short distance so the mouth is the only external opening through which moisture might be lost. By the time the mud is hardened, breathing is reduced to one gentle expiration and inhalation about every two hours. Aestivation may last a few years or only a season, during which time muscle tissue is used for food. No wastes are eliminated. The urea is separated from the water and stored. The water is used over and over again. Within twenty-four hours after the

lung-fish has come out of aestivation and been placed in water the concentration of urea is back to about normal. (Coates, 1937).

It was thought by some writers that Ceratodus and Lepidosiren were accustomed to go on land or at least on the mudflats. Gunther (1871) reports that any he has observed in captivity have shown no tendancy to leave the water. He also believes that the gills should be efficient for breathing when the water is of normal composition and sufficiently pure to furnish the necessary amount of oxygen. During this time, the gills alone take care of the respiratory function while the lungs receive arterial blood and return venous blood like all other organs of the body. But when the water becomes thick and muddy and charged with gases from decomposing organic matter, the fish begins to breathe with its lungs. Then the lungs receive impure blood and return purified blood to the heart.

In Protopterus and more so in Lepidosiren the gills are partially atrophied and this leads Bridges (Cam. Nat. Hist. Vol. 7) to believe that the lungs are the principal organs of breathing at all times, in contrast to Gunther (1871) who believes the gills normally do most of the work of respiration.

Lung Structure in Protopterus

The lung (Fig. 10) is double, although in the anterior third the two lungs are united by connective tissue. The

posterior parts are separate and extend the whole length of the body cavity, gradually tapering toward the cloaca. The unpaired part is continued as a vestibule or pneumatic duct which passes along the right side of the esophagus and opens into it by a ventrally situated glottis which is protected by an epiglottis-like fibro-cartilaginous plate. "The central cavity of each lung (Fig. 12) communicates with a series of larger or smaller alveoli in the lung wall, and each of the latter opens in succession into smaller tubular cavities, and then into still smaller terminal caecal sacculi." (Cam. Nat. Hist. Vol. 7).

The unpaired part of the lung is more highly specialized than the paired part where the network covering the inner surface projects inward only a short distance, leaving a definite atrium. In the unpaired part the entire cavity is filled in with the sponge-like network so the atrium cannot be distinguished.

The epithelial lining of the lung is composed of a single layer of rather flat cells in close relation to the blood vessels. The connective tissue supporting the blood vessels contains masses of smooth muscle fibers and numerous pigment cells. (Parker, W.N., 1892).

Concerning the question of the apparent twisting of the lungs W.N. Parker (1892) says, "The relation of the pulmonary branches of the vagus (Fig. 11), as well as the pulmonary arteries, seem to indicate that a twisting of these organs (the lungs) has taken place in the course of development, as they grow from

their point of origin on the ventral side to the dorsal side of the alimentary tract. Close to its exit from the skull each vagus nerve gives off a branch which passes backward and medially, so that on reaching the dorsal side of the proximal end of the lung it crosses its fellow and then runs backward along the dorso-lateral surface of the lung of the other side (Fig. 11, X pul.). Thus the right lung is supplied by the left vagus nerve and vice versa. This would seem to show that a twisting had taken place through an arc corresponding to a semi-circle."

Lung structure in Lepidosiren*

Lepidosiren closely resembles Protopterus in its lung structure. Of all the lung-fishes the gills have degenerated most in Lepidosiren. Therefore, it has well developed lungs and breathes air more frequently.

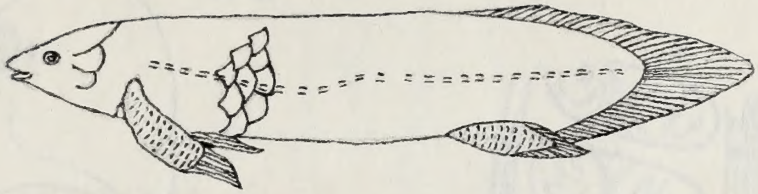
The lungs are paired with the anterior portions united to form a median chamber with a spongy character due to the numerous trabeculae. The pneumatic duct is a short wide membranous tube kept open by a laryngeal cartilage. The glottis is guarded by an epiglottis-like structure. At its posterior end, the trachea dilates into a membranous sac which communicates by two large lateral openings with the lungs.

The lungs are widest anteriorly and gradually taper, ending near the cloaca in a point. They are lodged in a dorsal angle

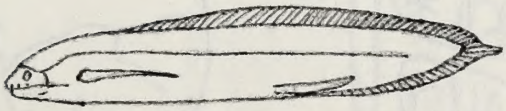
*From Owen (1839).

of the body cavity and are attached to all the surrounding parts and particularly to the ribs, whose impressions they bear.

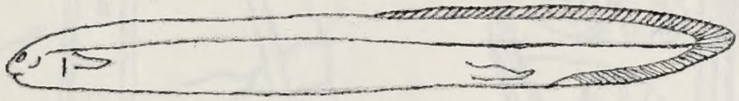
The anterior part of each lung is the most vascular, as its deeper color indicates. It is divided into four or five small lobes of which the first is about a half inch long, triangular in form, with the apex forming the most anterior part of the lung. The other lobes decrease in size. About an inch and a half from the anterior end, the lungs take the form of simple compressed bags and continue thus to their posterior extremities.



Neoceratodus fosteri. (From Newman.)



Protopterus annectans. (From Newman.)



Lepidosiren paradoxa. (From Newman.)

Fig. 7.—The three living genera of lung-fishes.

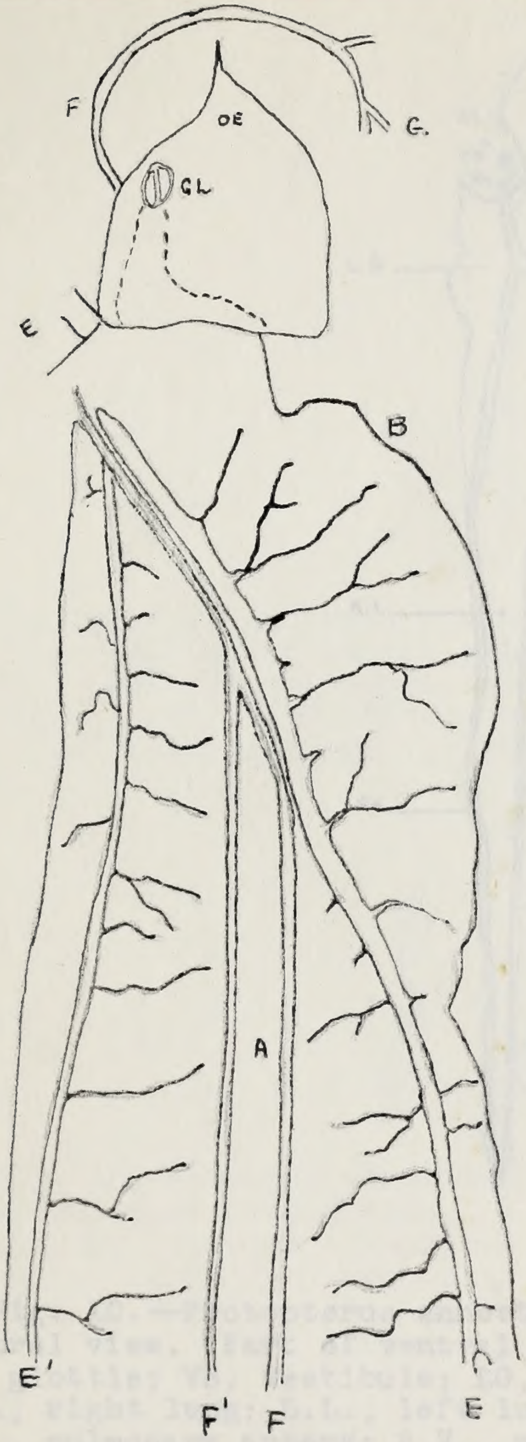


Fig. 8.—Ventral view of lung of Ceratodus.

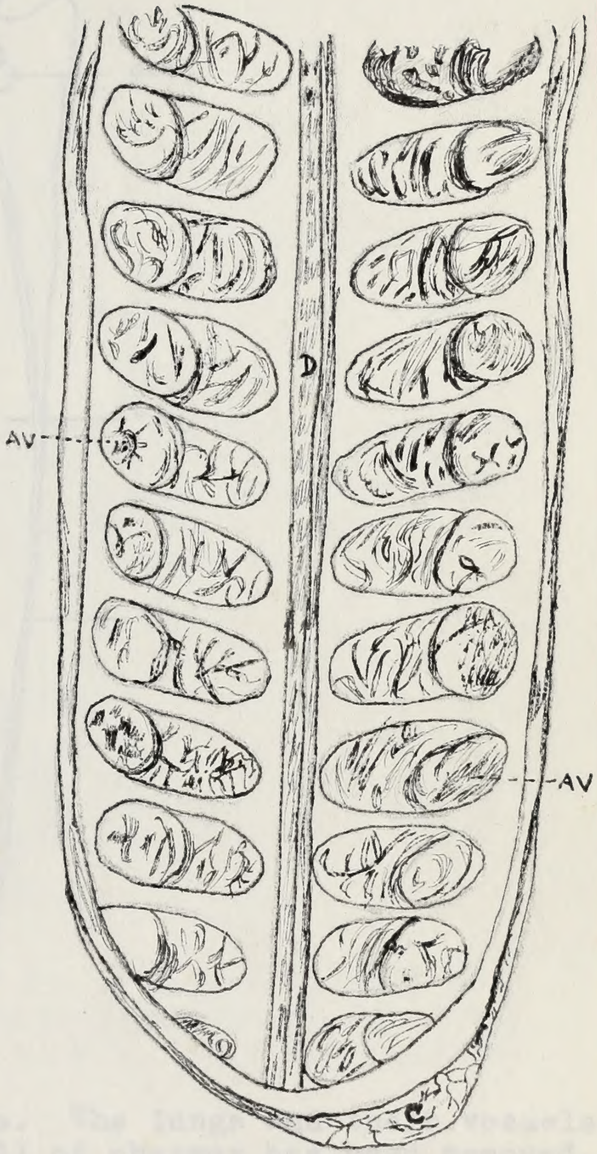


Fig. 9.—Interior of lung of Ceratodus cut open along smooth stripe in its median line.

A, stripe along middle of ventral surface; B, C, slight prominence indicating division of lung into two halves; D, dorsal fibrous band; AV, alveolus; E, E', pulmonary veins; F, F', branches of pulmonary artery; G, branches of F. (From Gunther.)

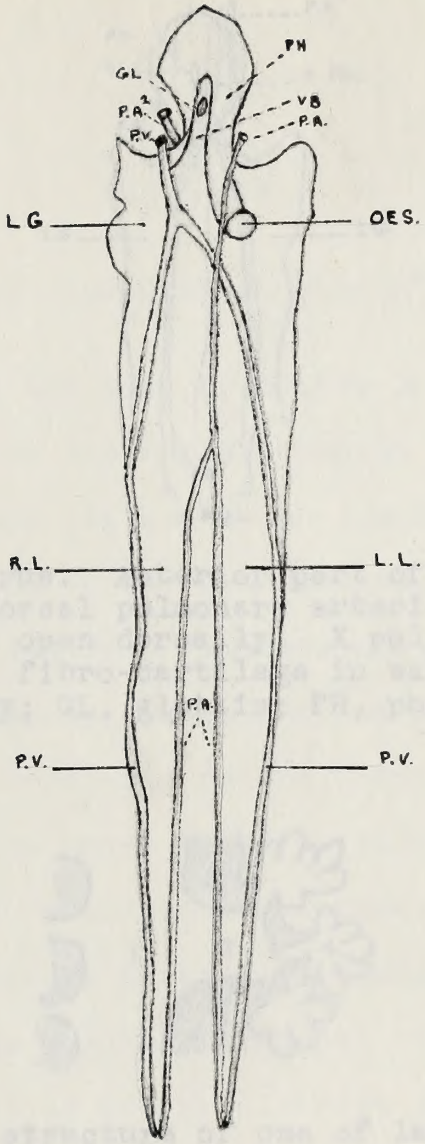


Fig. 10.—Protopterus annectans. The lungs and their vessels, ventral view. Part of ventral wall of pharynx has been removed. GL, glottis; VB, vestibule; LG, undivided portion of lung; R.L., right lung; L.L., left lung; PH, pharynx; OES, oesophagus, P.A., pulmonary artery; P.V., pulmonary vein. (From W.N. Parker.)

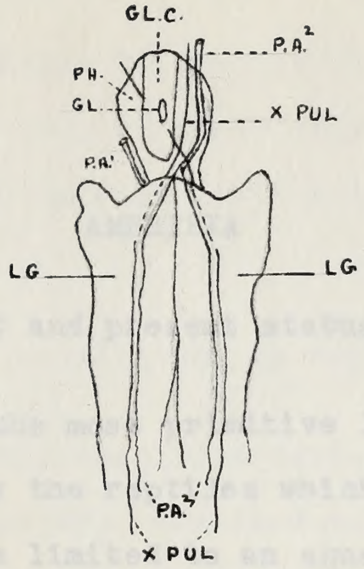


Fig. 11.—Protopterus. Anterior part of lungs, dorsal view, showing relation of dorsal pulmonary arteries and pulmonary nerves. Pharynx slit open dorsally. X pul, pulmonary branches of Vagus nerve; GL.C, fibro-cartilage in walls of glottis; P.A., pulmonary artery; GL, glottis; PH, pharynx. (From W. N. Parker.)

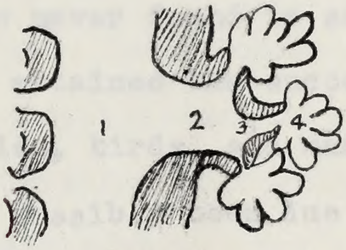


Fig. 12.—Showing structure of one of larger alveoli of air-bladder of Protopterus. 1. central cavity; 2. alveolus; 3. tubular cavities communicating with 4, the small terminal sacculi. (From Cam. Nat. Hist.)

AMPHIBIA

Past and present status*

The Amphibia are the most primitive land vertebrates but are closely followed by the reptiles which are much more terrestrial. Amphibia are limited to an aquatic medium during at least the developmental period in most groups, and during the entire life cycle in others. Fundamentally they are aquatic because their developmental processes are aquatic. Only a few of the most highly specialized modern forms lay their eggs out of water. Amphibia are never found in salt water (Weysse, 1911).

Amphibia have not attained the success and dominance reached by fish, reptiles, birds, and mammals. This lack of success as a group has possibly been due to their varied environment. They are forced to occupy a narrow strip of land between the water and dry land, a prey to fish on one hand and to reptiles, birds, and mammals on the other. If attacked in one environment they may seek the other and this has saved them from complete extinction. The Anura are well known, but the salamanders, newts and caecilians have sought safety in out of the way places and exist partly through their extremely retiring habits.

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*From Newman, 1924.

The change from aquatic to terrestrial life has been the greatest evolutionary crisis in vertebrate history. The most important changes had to do with respiration, circulation, and locomotion.

Types of respiration in Amphibia

Gills and lungs. All Amphibian larvae bear gills, but in different genera these organs vary in duration of existence, those of aquatic species keeping their external branchiae for a much longer period than the terrestrial forms. In a few Urodeles, for example, Proteidae and Sirenidae, the gills remain in the adult although the lungs also are functional. These animals are called perennibranchiate Urodeles. They are permanent water dwelling forms. Their lungs are less elaborate than those of the Dipnoi, having thin-walled sacs with no complicated alveolar structure to increase the respiratory surface which is poorly vascularized. Such simple lungs are compensated by extensive cutaneous and bucco-pharyngeal respiration.

In the Anura the gills are never retained in the adult. Toward the end of the second month after hatching, the lungs come into use and the tadpoles frequently come to the surface of the water to breathe. The gills then begin to degenerate but for a time respiration is carried on by both gills and lungs.

Without gills the lung structure becomes more complicated and improved by the development of alveolar cavities on the

inner surface which add greatly to the lung area for respiration. Noble (1931) described the alveoli in different groups as follows. "In the terrestrial Salienta (Anura) such as Bufo, these chambers are small and numerous, and the septa branch, forming additional chambers. The septa are highly vascular and clothed with a thin epithelium except along their inner edges where ciliate and mucous cells are abundant covering bundles of smooth muscle. In many aquatic Urodeles which practice extensive cutaneous and bucco-pharyngeal respiration, the lungs are poorly vascularized and alveoli not formed. This is true of some newts and especially the perennibranchs Proteus and Necturus."

Air-tubes

Generally in Amphibia the distinction between the air-tubes and truly respiratory region is not very pronounced. However, in Gymnophiona and some Urodeles (Siren and Amphiuma) the trachea is definitely formed with walls strengthened by paired cartilages in semi-circular form (Goodrich, 1930). In Amphibia the primitive trachea and bronchi enter the lungs at the extreme anterior end, whereas in higher forms with lungs better developed especially in the anterior part, the bronchi enter further back (Walter, 1928). Anteriorly the lungs of Anura open into a small laryngo-tracheal chamber which communicates with the mouth by a narrow longitudinal slit-like glottis, surrounded by rudimentary cartilages (Parker & Haswell, 1897).

Covering of the lungs

As a result of migration posteriorly, the lungs are covered by a single layer of peritoneum which was pushed ahead of them into the body cavity during development. They do not, therefore, have a pleural cavity of their own, but instead lie freely in the common body cavity (Walter, 1928).

Degeneration of lungs

In many Salamanders, for example, Salamandridae, Amblystomatinae, Desmognathinae, and Plethodontinae (Wiedersheim, 1897) the lungs undergo a more or less complete degeneration even though all traces of gills have been lost. The lung rudiments in Rhychatriton are 5 mm. long and in Salamandrina 2 mm. long (Noble, 1931). These salamanders breathe by gills until metamorphosis, but in the adult state resort to respiration by skin, bucco-pharynx and even the esophagus (Cam. Nat. Hist. Vol. 7). The fact that the floor of the mouth is continually raised and lowered as in Amphibia which possess lungs, and that in some cases the animal dies if these respiratory movements are prevented indicates that a bucco-pharyngeal respiration takes place and that cutaneous respiration alone is insufficient (Wiedersheim, 1897). "In various species and genera of the family Salamandridae the lungs, trachea, and larynx have entirely vanished in the lungless salamanders, being represented by merely a depression on the floor of the esophagus in the embryo and even this may

disappear in the adult" (Goodrich, 1930). "Salamanders are the only vertebrates above the fish which have succeeded in dispensing with their lungs" (Noble, 1931).

Tracheal lungs

In Typhlonectes, an aquatic form, another variation appears in the form of a tracheal lung or respiratory surface along the passage-way between the lung and the pharynx, a condition found typically in some snakes (Noble, 1931).

Hydrostatic function of lungs and ypsiloid apparatus*

The lungs of certain salamanders have a hydrostatic function as well as a respiratory function. In Proteidae, also, the lung is hydrostatic rather than respiratory.

Closely correlated with the hydrostatic function of the lungs is a structure called the ypsiloid apparatus, found in many salamanders. It is a "Y" shaped cartilage, movably articulated to the anterior edge of the pubis. The action of the ypsiloid apparatus has been studied by Whipple, especially in the American salamander, or newt, Diemyctylus (Triturus) viridescens. This salamander which is the most aquatic of all American salamanders can swim slowly or rapidly, float, remain suspended in the water, walk on the bottom, or paddle by all four feet. The changes in buoyancy required for this versatility are

*From Whipple (1906).

accomplished partly by the lungs. The salamander swims to the surface and takes in air sufficient to cause the body to float. Increase in buoyancy is usually followed by the emission from the lungs of one, two, or three bubbles of air, until buoyancy is perfectly adjusted. Still more air is emitted before sinking to the bottom.

The animal is furthermore able to change the direction of the long axis of the body without the slightest swimming motions. This is accomplished by a noticeable change in the shape of the body. When the head is slanting downward there is a pronounced bulging of the lateral and ventral walls of the posterior third of the body, especially noticeable in the angle between the ilium and the vertebral column, as though pressure from within were being exerted. As the body swings upward, there occurs a marked constriction in this part of the body, that is, in the ypsiloid region.

The lungs of Diemyctylus are sacs that extend the entire length of the body cavity, a fact which can be demonstrated by inflating the lungs of a freshly killed specimen. They are narrow anteriorly, widen gradually, and round off abruptly at the posterior end like a club. The free posterior end of each lung lies in the angle between the ilium and the vertebral column and when inflated, causes the bulging of the lateral and ventral walls. If inflation is not accompanied by muscular constriction, this part of the body becomes relatively more buoyant, causing

the head region to slant downward. As soon as the ypsiloid apparatus acts, the resulting pressure on the posterior abdominal region becomes exerted on the club-like ends of the lungs and forces the air in them forward. The effect is to increase the buoyancy of the anterior region. On the other hand, when the muscles relax, the pressure of air in the lungs as well as the elasticity of all parts concerned, allows air to return to the posterior region again.

Thus the ypsiloid cartilage and the muscles connected with it, together, with the lungs, constitute the mechanism by which the relative buoyancy of the anterior and posterior ends of the body may be regulated.

"The ypsiloid apparatus with the exception of Cryptobranchus is confined to the Salamandrida." "In Plethodontidae and Desmognathidae in which the lungs have wholly degenerated a corresponding degeneration of the ypsiloid cartilage has occurred ..." (Whipple, 1906).

Whipple found no ypsiloid cartilage in Necturus maculatus, Amphiuma means, and Siren lacertina.

Cutaneous respiration

No Amphibian has sufficient lung surface to complete the aeration of the blood (Adams, 1933). Therefore, a cutaneous system is required to supplement the lung action. Aquatic Amphibians, although acquiring oxygen principally through the

lungs, give off carbon dioxide which has great solubility in water, largely through the skin. This has been proven in many experiments by S. H. and S. P. Gage (1886) who summarize as follows "... the respiratory gas-interchange in combined aerial and aquatic respiration does not conform to the law governing either exclusively aerial or exclusively aquatic respirations, but that whenever aerial and aquatic respirations are combined in an animal, the aerial part is principally to supply oxygen, and the aquatic part to get rid of carbon dioxide."

Amphibia have abundant skin glands secreting moist mucus which keeps the skin in proper condition for respiration and helps it to retain its flexibility. The skin is kept moist in the frog because it frequently immerses itself in water (Newman, 1924).

The capillaries in Amphibia with rudimentary lungs either penetrate into the epidermis to facilitate cutaneous respiration, or else the epidermis remains thin over the skin capillaries. An ideal habitat for cutaneous respiration on land is the cool wet crannies along banks of streams where there is opportunity to keep the skin moist. Therefore, stream salamanders never have the lungs well developed. (Noble, 1931).

Bucco-pharyngeal respiration

All Amphibia practice cutaneous respiration and most practice bucco-pharyngeal respiration in either air or water. For this reason the linings of the mouth and throat are very

vascular. (Noble, 1931).

Mechanics of respiration

In Amphibia the lungs are filled according to the principle of the force pump, whereas in all higher forms they are filled by action like that of a suction pump (Goodrich, 1930).

Whipple (1906) explains the mechanics of respiration as follows. Pulmonary and bucco-pharyngeal respiration go on at the same time. Bucco-pharyngeal respiration takes place constantly and with such rapidity that the visible effect is a rapid fluctuation of the throat. The process begins with enlargement of the bucco-pharyngeal cavity by lowering the hyobranchial apparatus. This results in air being drawn in through the nares. Following this inhalation is an exhalation in which the floor of the mouth rises. The mouth remains tightly closed during the entire process and the respiratory currents make use of the nasal passages alone.

At frequent, though irregular intervals during bucco-pharyngeal respiration, acts of pulmonary respiration occur. The floor of the mouth is prolonged and exaggeratedly depressed. The nares close more or less completely. Air is drawn from the lungs into the mouth through the open glottis so the air in the mouth becomes a mixture of pure and impure. When the floor of the mouth is raised again some of this mixed air is forced into the lungs and some out through the nares.

In addition to aerial bucco-pharyngeal and aerial pulmonary respirations there is aquatic respiration in which water is drawn in through the nares, and expelled through the mouth and nares. Animals change from one system to another as necessary, but it is difficult to make a rapid change, especially if the animal has been in one medium for a long time. Some lunged salamanders, notably Diemyctylus, come to the surface to gulp air, thereby getting a larger quantity quickly.

Gnanamathu (1936) has done many experiments with mechanics of respiration in the frog (Fig. 13). He, like Whipple, believes that bucco-pharyngeal respiration is not interrupted for pulmonary respiration but that the two types go on simultaneously. The lungs are compressed by the contraction of the body wall so that expiration of air from the lungs into the buccal cavity is due partly to this and partly to sucking action caused by lowering the floor of the buccal cavity.

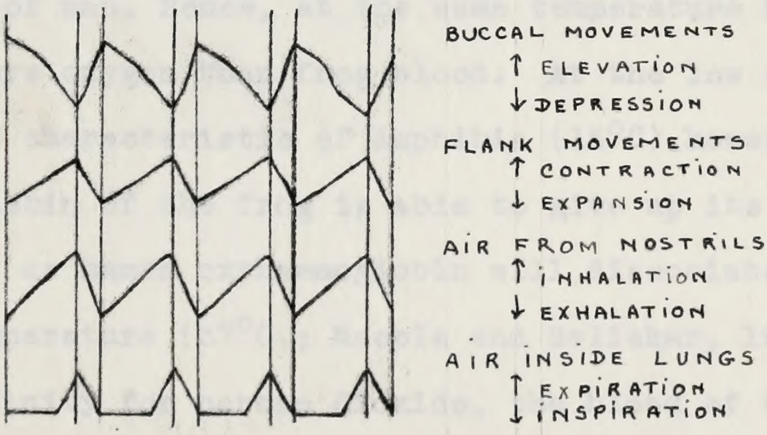

Fig. 13.--Scheme of records to show synchronism of various movements concerned in respiration in the frog. (From Gnanamuthu)

Characteristic of this mode of respiration in which the ribs take no part, is the great modification in the ribs. In no living Amphibian do they meet at the sternum (Goodrich, 1930).

Hibernation

The ability of the frog to breathe through the skin enables it to hibernate. Then it can get only the oxygen taken in through the skin and oxidation goes on just fast enough to keep the animal barely alive. The cold, by slowing down metabolism, reduces the need for oxygen. Hence, frogs can survive under water for long periods, but will die if the temperature is raised. Cold seems to have been an important factor in permitting lung reduction in Ascaphus, America's most primitive frog, since other stream-dwelling frogs who live in warmer waters have larger lungs. (Noble, 1931).

"The affinity of frog haemoglobin for oxygen is much lower than that of man. Hence, at the same temperature human blood takes on much more oxygen than frog blood. At the low temperature ordinarily characteristic of Amphibia (15°C) however, the oxyhaemoglobin of the frog is able to give up its load of oxygen as readily as human oxyhaemoglobin will dissociate at a much higher temperature (37°C.; Macela and Seliskar, 1925). In regard to its affinity for carbon dioxide, the blood of the bullfrog as compared with mammals binds a comparatively high amount (Wastl and Seliskar, 1925) but is unable to regulate its alkalinity as effectively as mammalian blood does." (Noble, 1931).

Respiration in Specific Amphibia

In addition to the general information on Amphibia, the following animals are treated in detail.

- Apoda (Gymnophiona or Caecilia)
- Urodela (Caudata)
    - Salamandridae
        - Species Diemyctylus (Triturus) viridescens
    - Proteidae
        - Species Necturus maculatus
- Anura (Salienta)
    - Ranidae

APODA (GYMNOPHIONA OR CAECILIA)

This is a very degenerate group with burrowing habits like the earth-worms. It inhabits tropical or subtropical regions. It has no limbs and a very rudimentary tail (Fig. 14). The skin is arranged in ring-like folds, and is smooth and shiny, set with small dermal scales. The eyes are small and concealed under the skin or maxillary bones, and are practically functionless.

The gills are lost when the larva hatches. The adult lives a burrowing life on land. The right lung is elongated, with the inner surface divided by a network of blood-vessels, connective tissue, and smooth muscle, which form alveoli. The left lung is rudimentary, being only a few millimeters long. The reduction of one lung occurs also in snakes and seems to be correlated with the elongate body form of both groups. (Noble, 1931).

The trachea is very long, and its walls are strengthened by a series of paired cartilages, each of which extends about half way around the trachea.

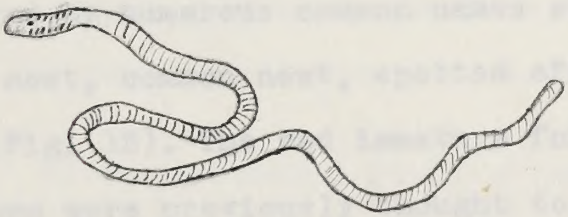

Fig. 14—Gymnophiona. (From Adams.)

URODELA (CAUDATA)

This group includes all the tailed Amphibia, more than 100 species of mudpuppies, newts, efts, salamanders. They vary from forms living permanently in water and breathing by external gills in addition to lungs, to forms that live after metamorphosis entirely on land, especially in moist woods or other sheltered places.

SALAMANDRIDAE

The Salamandridae include the salamanders and newts which comprise three-fourths of all the tailed Amphibia. They have no gills in the adult stage. Fore and hind limbs are present but much reduced. Salamanders are usually completely terrestrial in the adult stage while newts have aquatic tendencies throughout life.

Diemyctylus viridescens (Raf.)

Relation of life history to respiration*

This species is well known also by the name Triturus viridescens, and by numerous common names such as spotted salamander, water newt, common newt, spotted eft, and vermillion-spotted newt (Fig. 15). The red immature form and the adult viridescent form were previously thought to be different species.

*From S.H. Gage (1891). He includes a long list of synonymous technical names.

It is the best known newt east of the Rocky Mountains, and the adult is the most aquatic of all American salamanders. It is but four inches in length including the tail which is long and spade-shaped.

The life history of this newt naturally influences the methods of respiration. In the beginning of the larval life, respiration is wholly aquatic, but as the lungs develop it gradually changes to a mixed or combined respiration, that is, to a respiration partly aerial and partly aquatic. Later when the larvae leave the water for a time and become terrestrial, respiration becomes wholly aerial. At this time, the stratified non-ciliated oral epithelium found in both larvae and aquatic adults gradually changes to ciliated epithelium. When an adult aquatic form is kept in air for ten days to two weeks, the epithelium of the mouth becomes ciliated like that of proper aerial forms. At egg-laying time the newt enters the water and respiration again becomes mixed. This shows the direct relation of the character of the oral epithelium to the mode of respiration. The adult newt under favorable conditions does not leave the water after entering it, although it is able to live for several months and perhaps indefinitely in moist places.

Bucco-pharyngeal respiration

If a terrestrial Diemyctylus is observed carefully, the floor of the mouth and pharynx will be seen to sink and rise alternately, many times per minute. On entering the water

Diemyctylus remains under for a considerable length of time and during this submergence the same rhythmical pharyngeal movements occur, and water instead of air is alternately taken into and expelled from the mouth.

Lung structure*

The lungs are two long, narrow transparent, membranous sacs which extend far back in the body cavity above the other viscera. Internally, each lung is a simple sac with no septa, so the external surface is smooth and shows no depressions. A layer of the peritoneum holds the anterior parts of the lungs in place but the posterior halves are free.

The layers of the lungs are represented in Fig. 16. They consist of (1) an outer serous coat composed of squamous epithelium. A few branched pigment cells are found in this coat, especially along the course of the pulmonary vein. (2) Inside the serous coat is a small quantity of white fibrous connective tissue, containing a meshwork of elastic fibers. (3) A layer of non-striped muscle of nearly uniform thickness completely encircles each lung. The individual muscle cells are large and fusiform in shape, with a well defined nucleus. (4) The nerves are distributed abundantly throughout the muscular coat. (5) The capillaries in the pulmonary walls lie internal to the muscular layer. (6) Internal to, and distributed among the capillaries

*From Stirling (1881).

are the epithelial cells forming the innermost layer of the lung. Distributed throughout the epithelium are definite tracts of cilia, especially along the course of the pulmonary vein and its chief branches. Williams (1859) claims ciliated epithelium is present over the course of the pulmonary artery but Stirling disagrees.

The non-ciliated epithelium consists of flattened cells with large globular nuclei. The cells are arranged in groups and the large nuclei occupy the small meshes between the capillaries, while the thin parts of each cell cover the capillary wall. The result is that the air in the lung is separated from the blood by the thin non-nucleated part of these cells and the flat cells that form the capillary wall.

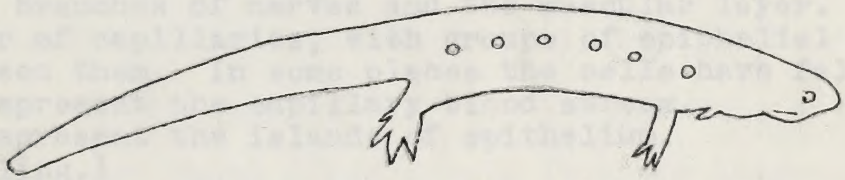

Fig. 15.—Diemyctylus viridescens. (From Hegner.)

Fig

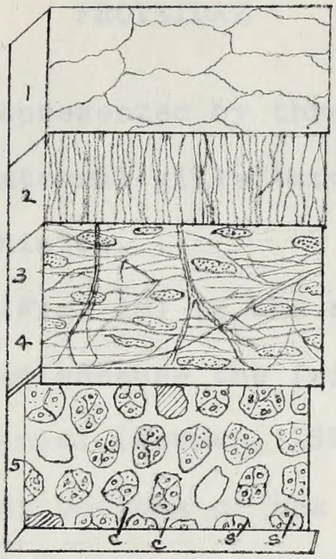

Fig. 16

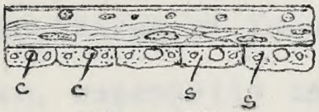

Fig. 17

Fig. 16.—Scheme of the wall of the lung of the newt, showing layers from without inwards.

1. Serous coat—squamous epithelium.
2. Layer of elastic tissue imbedded in a small quantity of connective tissue.
3. & 4. Branches of nerves and the muscular layer.
5. Layer of capillaries, with groups of epithelial cells between them. In some places the cells have fallen out.

C, C, represent the capillary blood stream.
S, S, represent the islands of epithelium.
(From Stirling.)

Fig. 17.—Scheme of a vertical section of the wall of the lung.

C, C, represent capillaries.
S, S, represent arrangement of pulmonary epithelium.
(From Stirling.)

PROTEIDAE

The Proteidae are represented by three species all bearing three pairs of fringed external gills throughout life and therefore called perennibranchiates.

Necturus maculatus (Fig. 18) is the common American water dog or mudpuppy, so called because the fringed gills resemble the hairy ears of a water spaniel (Newman, 1924). Necturus leads a sluggish life on the muddy bottoms of the Great Lakes and the rivers of the Mississippi Valley, and is most active at night when it swims or crawls in search of food. It closely resembles the larva of Salamandridae, especially that of Ambystoma (axolotl).

Proteus anguinus (Fig. 21) a European species, is restricted to the subterranean waters of Carniola, Carinthia, and Dalmatia. It lives much below the surface, in absolute darkness, in an almost constant temperature of 50° F. As a rule, in captivity it remains motionless under water, but if the water is not sufficiently aerated, it rises to the surface, gives off a bubble of air, and takes a new supply into the lungs. In Proteus the eyes are completely hidden beneath opaque skin (Newman, 1924). In Necturus the eyes are functional, being covered by a thin, transparent skin.

Typhlomolge rathbuni is much like Proteus. It inhabits subterranean caves and was discovered in artesian wells in Texas (Newman, 1924).

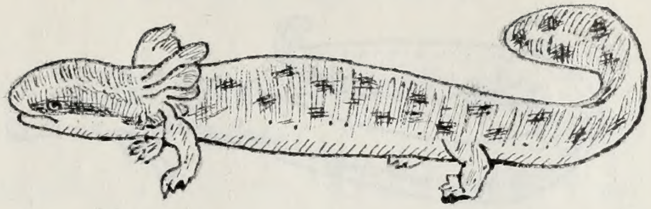

Fig. 18.—Necturus maculatus. (From Newman.)

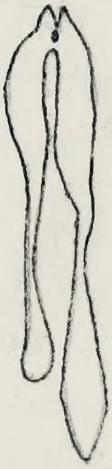

Fig. 19.—Lungs of Necturus. Communication with the vestibule indicated by a black spot anteriorly. (From Wiedersheim.)

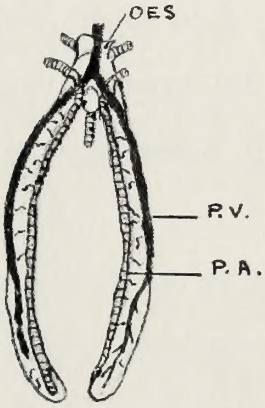

Fig. 20.—The blood vessels of the lungs of Necturus.
OES, oesophagus
P.A., pulmonary artery
P.V., pulmonary vein
(From W.S. Miller.)

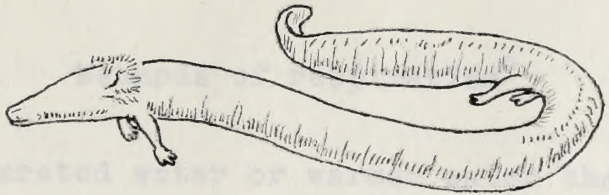

Fig. 21.—Proteus anguineus. (From Newman.)

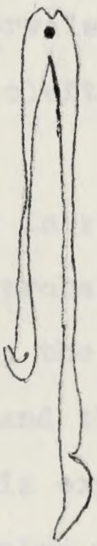

Fig. 22.—Lungs of Proteus. Communication with the vestibule indicated by a black spot anteriorly. (From Wiedersheim.)

Necturus maculatus

Methods of respiration*

In poorly aerated water or warmer water than the animal is accustomed to, the gills are kept in constant motion. In clear, cold, well-aerated water, they are often held motionless against the sides of the neck for long periods. Under such conditions the blood supply is reduced, and the gills change from bright to dull red. When the oxygen supply is low, Necturus rises to the surface at frequent intervals to gulp air, part of which passes out through the gill clefts and the remainder into the lungs.

The skin also functions in respiration and is well supplied with blood. The skin alone probably furnishes the necessary oxygen in well-aerated water; the gills are used under ordinary lake and stream conditions; and the lungs called into service last. If a living specimen is exposed to the air, it dies in a few hours, the lungs alone being unable to furnish sufficient oxygen. In water, however, the animal may live without apparent discomfort with gill filaments entirely lost.

*From Bishop (1926).

Structure of lungs*

The lungs consist of two narrow elongated transparent membranous sacs (Fig. 19). Along the outer mid-line of the lung the vein is located (Fig. 20) and on the inner side the artery. Lateral branches with capillaries are arranged so that there is an arterial branch located between every two venous branches.

The lungs extend back into the abdominal cavity dorsal to the other viscera. They are attached along most of their length to the dorsal wall. The full grown lung when distended is 100 to 125 millimeters long, of which less than 25 millimeters is free.

Internally, the lungs are typical of all urodeles, being perfectly simple sacs, with no septa developed. Their cavities open into the pharynx through a membranous tube which represents the trachea of higher vertebrates.

Serous layer

The cells of the epithelium which forms the outermost or serous layer of the lung vary in different parts of the lung, as illustrated in Figs. 23, 24, and 25.

*From Miller (1900).

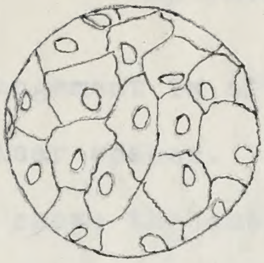

Fig. 23

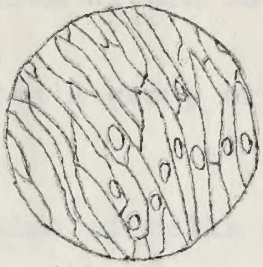

Fig. 24

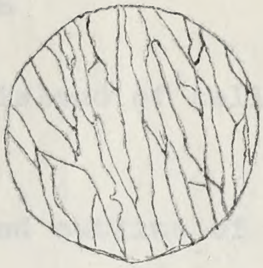

Fig. 25

Fig. 23 represents the epithelium found between the large blood-vessels, especially in the anterior part of the lung. This is the common type, consisting of large thin irregular cells with comparatively smooth boundaries. The nuclei of these cells have no definite location but may be found in any part of the cell.

Fig. 24. Epithelial cells near the large blood-vessels and toward the posterior end of the lung are longer and narrower, becoming more so toward the tips of the lungs. Between the lateral branches of the blood-vessels there are often whorls of cells centering around a large irregular one.

Fig. 25. Covering the blood-vessels and lymphatics is an entirely different type of epithelial cell. It is often extremely long and always has jagged edges.

Along the inner side of the lung near the pulmonary vein, oddly shaped pigment cells are often present.

Between these three typical cells are all gradations.

Epithelium within lung

The arrangement is often a group or island of cells surrounded by clear spaces.

Fig. 26 shows the outline of cells and outline of the islands in which the nuclei and the protoplasmic part of the cells are situated.

Fig. 27 shows relation of nuclei and protoplasm to cell boundaries in a case where several nuclei are found in a single mesh of capillary network.

Fig. 28. Sometimes a single cell forms an island.

Fig. 29. Cell boundaries appear to cut through the nucleus of a neighboring cell due to overlapping of one cell by another.

Fig. 30 is a projection drawing of two cells from Fig. 29 showing the relation of cell boundaries to nucleus and to underlying capillaries.

Ciliated epithelium and a plexus of capillaries were found over both the artery and the vein, down to the apex of the lung, while a few ciliated cells were found between them.

Elastic fibers

Elastic fibers are found throughout the walls of the lungs forming a complex network with coarser fibers and wider meshes near the surface and finer fibers located more deeply. The coarse fibers run more generally in a direction parallel to the

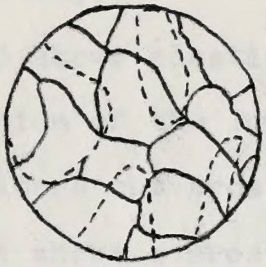

Fig. 26

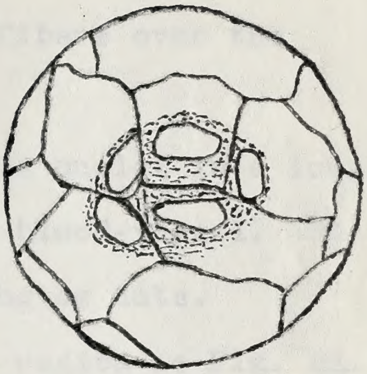

Fig. 27

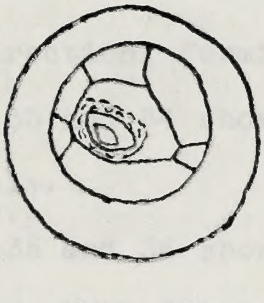

Fig. 28

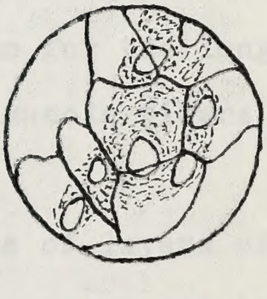

Fig. 29

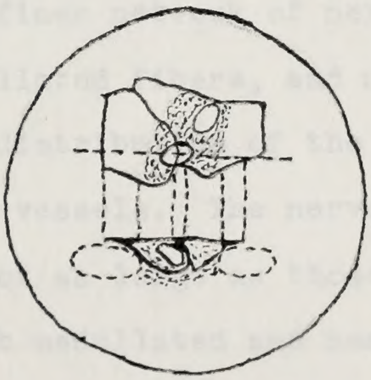

Fig. 30

long axis of the lung. The meshes of the fine fibers are very intricate, especially around the blood-vessels.

Fig. 31 is a surface view of elastic fibers over the pulmonary artery.

Fig. 33 shows elastic fibers and muscle nuclei in a longitudinal section of the lung taken near the blood-vessel. It shows the fibers cut crosswise and appearing as dots.

Fig. 34 shows a cross section in same region as Fig. 33. The fibers cut lengthwise appear as lines.

Muscle fibers

These are of the involuntary type and run principally in a circular direction, forming a tubular foundation for the lung.

Figs. 33 and 34 show the relation between muscle fibers and blood-vessels.

Figs. 35 and 36 show the relative thickness of layers of muscle fibers both internal and external to the artery and the vein.

Nerve fibers

Fig. 32 shows the finer network of nerve fibers with medullated and non-medullated fibers, and nerve cells.

Fig. 37 shows the distribution of the main nerve trunks found between the blood-vessels. The nerve trunks lying over the blood-vessels are not as large as those forming the meshwork between them. Both medullated and non-medullated fibers are found in the main trunks.

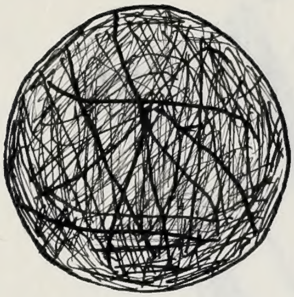

Fig. 31

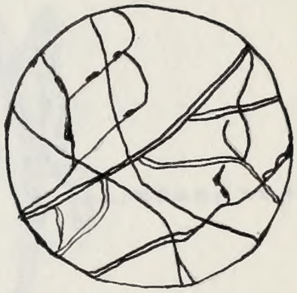

Fig. 32

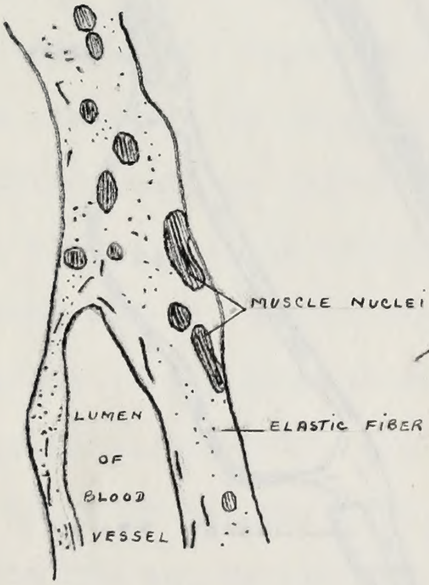

Fig. 33

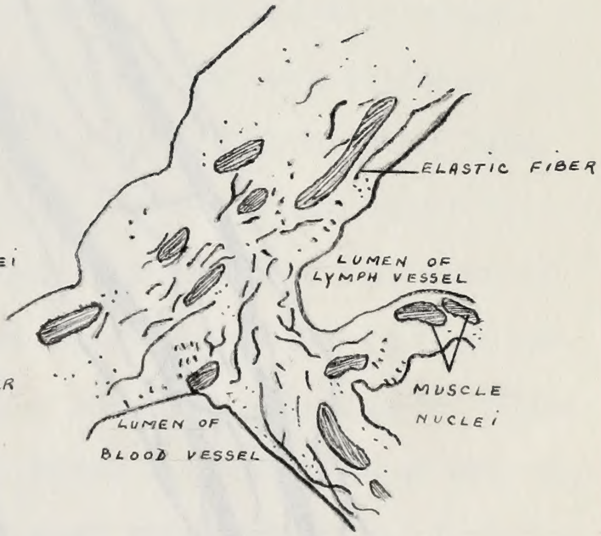

Fig. 34

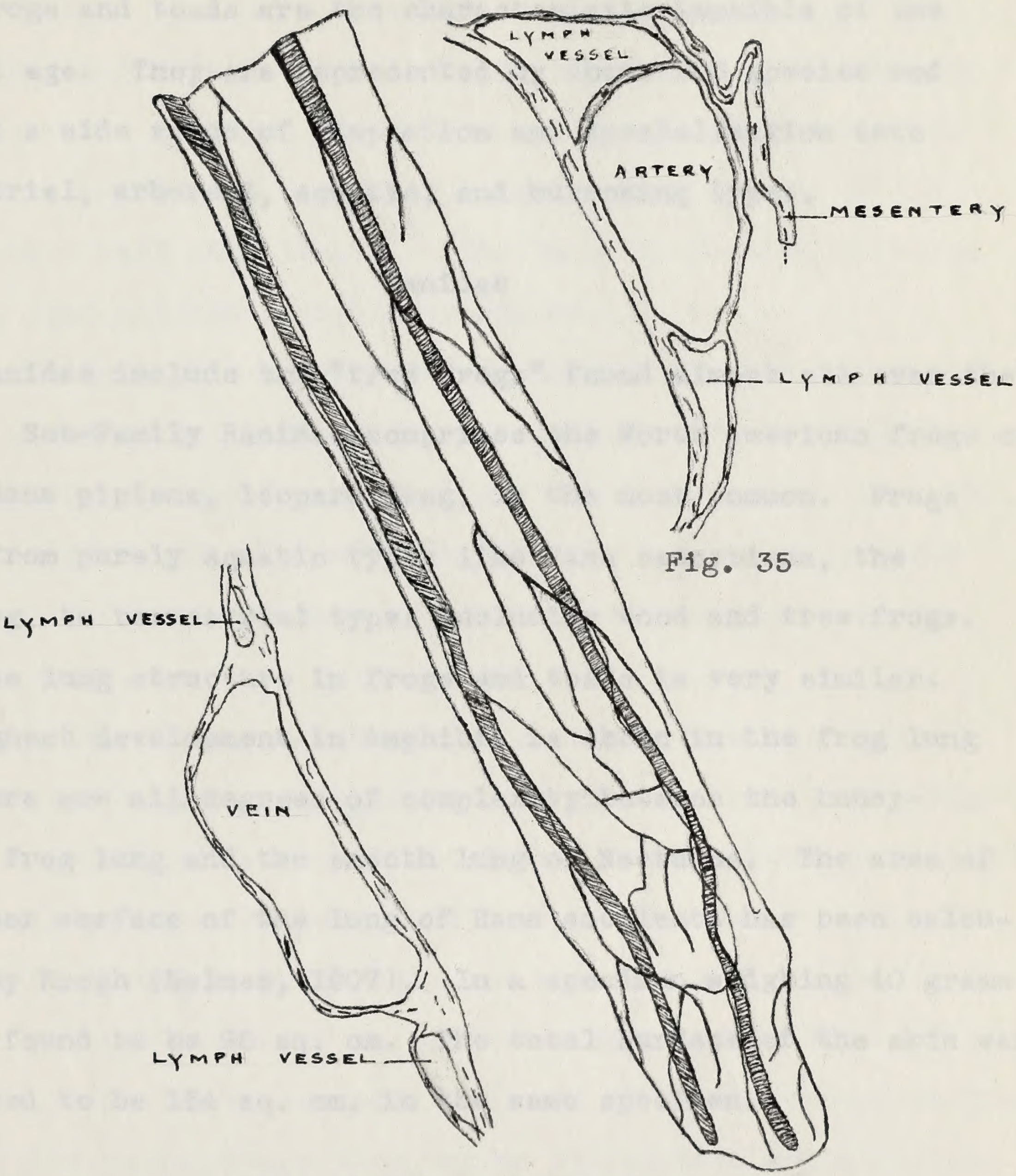

Fig. 35

Fig. 36

Fig. 37

ANURA (SALIENTA)

Frogs and toads are the characteristic Amphibia of the present age. They are represented by about 900 species and exhibit a wide range of adaptation and specialization into terrestrial, arboreal, aquatic, and burrowing types.

Ranidae

Ranidae include the "true frogs" found almost all over the world. Sub-Family Raninae comprises the North American frogs of which Rana pipiens, leopard frog, is the most common. Frogs range from purely aquatic types like Rana catesbiana, the bullfrog, to terrestrial types including wood and tree frogs.

The lung structure in frogs and toads is very similar. The highest development in Amphibia is shown in the frog lung but there are all degrees of complexity between the honeycombed frog lung and the smooth lung of Necturus. The area of the inner surface of the lung of Rana esculenta has been calculated by Krogh (Holmes, 1907). In a specimen weighing 40 grams it was found to be 98 sq. cm. The total surface of the skin was estimated to be 154 sq. cm. in the same specimen.

Lung structure in Anura

The lungs are large paired thin-walled sacs, spherical in shape to conform to the body form (Fig. 38). They vary greatly in size and appearance according to their state of distention.

With the exception of their roots they lie entirely free in the body cavity and are covered by the pleuro-peritoneal membrane. This is true of most forms except the toads Pipa and Xenopus which have a so-called diaphragm attaching the lung to the body wall. In Pipa, a considerable length of the lung is firmly attached to the body wall. In Xenopus, a fold of the peritoneum a half inch long ties the lung to the body wall and there is also a pulmo-gastric attachment.

The folds within a frog's lungs extend from the inner wall in such a way as to divide the entire cavity into stall-like air-chambers, all opening freely into the lung cavity (Fig. 38). The walls within the stalls become further increased by minor folds, each of which carries its individual capillary supply. (Walter, 1928).

In toads, the air-chambers are shut off from the central cavity of the lung by septa at right angles to their walls(Fig.38) so that a second internal wall is formed, whose openings lead from the central cavity. (Walter, 1928). The air-chambers are more extensively developed in correlation with the more terrestrial habits. The inner surface is covered with a single layer of epithelial cells which are very thin and flattened except on the edges of the septa, where they become cylindrical and ciliated. Outside the epithelium is a connective tissue layer which contains lymph and blood-vessels, and numerous unstriated muscle cells which give the lungs their power of contraction. The outermost surface is covered with peritoneum.

Minute structure of lung of frog[*]

1. Muscle tissue is arranged mostly in bands which form a coarse network of well-developed involuntary muscle fibers on the deeper surface of the lung. From this network of muscle bands, finer processes of muscle tissue pass towards the surface of the lung, and are attached to the thin and incomplete muscle layer found in the wall of the lung. (Fig. 39).

2. Connective tissue is present only in a small quantity, but sufficient to fill in the spaces between the various muscle bands and the surface of the lung. Through this connective tissue are distributed the blood-vessels, nerves, lymphatics, and numerous yellow elastic fibers. The lungs are extremely elastic and are capable of slowly expelling the air even after removal of the abdominal walls. This is a sort of substitute for ribs and other accessory organs of breathing (Williams, 1859).

3. Blood-vessels. The pulmonary artery lies just beneath the peritoneal epithelium and extends along the outer surface of the lung to the apex, giving off at right angles branches which divide and form a capillary network. This network has very small polygonal-shaped meshes, the diameter of which is often less than that of the adjacent capillary. From the capillary network branches arise that form the pulmonary vein which extends from the posterior tip of the lung to its roots. The lymphatics form a network surrounding the larger blood vessels. Pigment cells are numerous, large, and branched. They accompany the lymphatics

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[*] From Ecker (1889).

but not the blood vessels. The nerves of the lung follow the larger blood vessels under the serous coat.

In the lungs of the frogs and toads the septa have two layers of capillaries, one on either side. Thus the blood is exposed to oxygen on one side only. This fact constitutes an anatomical difference between the lungs of Amphibia and Reptilia, and those of mammals. In the latter case the septa are composed of a single layer of cells, both sides of which are exposed to the air. In this way, the amount of respiratory surface is doubled.

4. Epithelium. Externally the lungs are covered with a layer of endothelium derived from the peritoneum. The internal surface is covered with epithelium which varies greatly in different positions.

The capillary areas where respiration actually takes place (Williams, 1859) are covered only by a hyaline epithelium. The ciliated epithelium is limited to the course of the larger blood-vessels and the margins of the cells.

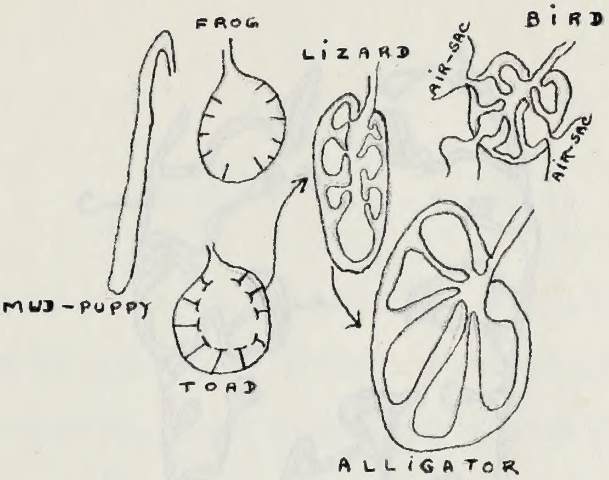

Fig. 38.—Diagrams to show evolution of lung structure. The plan of a lizard's lung may be regarded as like a cluster of toads' lungs, and in turn the alligator lung as composed of several lizards' lungs. The air-sacs of the bird extend beyond the lung itself but are in communication with it. (From Walter.)

39

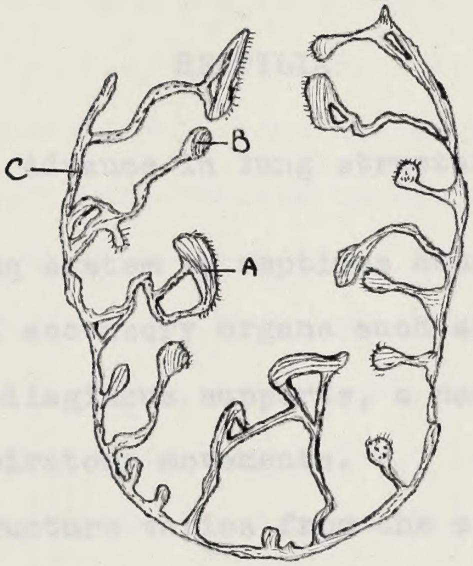

Fig. 39.—Outline of part of lung of frog, showing location of muscle tissue.
A, larger bands of muscle tissue.
B, smaller bands of muscle tissue.
C, incomplete muscle layer in wall of lung.
(From Ecker.)

REPTILIA

Advance in lung structure

The breathing system in reptiles consists of lungs aided by well developed accessory organs such as pharynx, larynx, a trachea with cartilaginous supports, a nasal passage, and ribs which aid in respiratory movements.

The lung structure varies from the simple sac with a large atrium, as seen in Sphenodon, to the mammalian type of lung found in all Amniota from crocodiles upward. The snake's lung exhibits variation in structure, being most complicated at the anterior end and most degenerate or sac-like at the posterior end. Only in the anterior region are the air-cells arranged in groups to form air-sacs.

Several advances in structure may be pointed out in a single animal such as the lizard, Heloderma suspectum. (1) The central cavity is divided by partitions into air-sacs which are subdivided into air-cells (Fig. 81, in summary). (2) The bronchus extends into the lung as far as the posterior sac. (3) Only the posterior sac is simple in structure as compared with the snake's lung in which about two-thirds is smooth and sac-like. (4) The atrium is reduced to a narrow tube because the air-sacs have encroached on the central cavity. This atrium is similar to a

bronchus except that it is perforated with the openings of the air-sacs.

Further advance is found in a higher lizard, Varanus, in which there is no atrium, a bronchus that subdivides into smaller tubes leading to infundibula, and a spongy texture throughout.

Turtles exhibit much variety in the amount of division into air-sacs and subdivision within these sacs, especially in the posterior chamber which may be as smooth as in Necturus, somewhat subdivided as in the frog, or complex in structure as in the rest of the lung, a condition found in Macrochelys. Each air-sac communicates with the bronchus by an oval or circular opening in its walls, as in Heloderma suspectum.

The highest approach to the mammalian type of lung is found in Crocodilia. The bronchus enters the lung near its center and passes somewhat obliquely to about the lower third where it divides into 8 to 15 tubes which are connected with numerous air-sacs (Fig. 81). A crocodile lung is like an enlarged lobule of a mammalian lung.

Stricker (1872) summarizes the condition of the bronchus in reptiles as follows: "The continuation of the bronchus, which projects a greater or less distance into the lung, consists in snakes of a semi-cylinder, in turtles of a straight tube perforated with round openings, and in crocodiles of a somewhat branching tube."

The trachea is strengthened by a series of cartilaginous rings, incomplete dorsally. In Reptilia with two lungs, the

trachea divides into two bronchi. Where only one lung is well developed, as in snakes, the trachea leads into the main lung, and an orifice in it just before that point admits air to the rudimentary lung. In snakes, the trachea sometimes extends into the lung as a groove called the tracheal gutter, which is often much reduced and represented by simply a flat band.

The lungs of Chelonia and Crocodilia differ from those of the other Reptilia in not projecting freely into the body cavity, because folds of the peritoneum separate them from it.

Asymmetry of lungs

In limbed and in some limbless Squamata the lungs are developed equally on both sides, but the long narrow body of snakes and of some lizards causes a crowding and displacement of some of the organs, resulting in asymetrical lungs. Cope (1894) examined 150 species of snakes. Butler (1895) investigated the lungs in 59 species of snakes belonging to 9 different families and in 21 species of lizards. Coe, in Coe and Kunkel (1906), studied the lungs of the anguoid Anniella pulchra. Both Coe and Butler checked the work of Cope and the results obtained show that in all forms except the Amphisbaenidae the left lung is the one that is reduced. In the Amphisbaenidae alone the right lung is reduced or absent. In snakes the well developed lung usually extends the whole length of the body cavity.

Mechanics of respiration

In some reptiles there is found the first evidence of fully developed ribs attached to the sternum in front and used as a mechanism of respiration. Inflation is brought about by the expansion of the thoracic chamber where the ribs, except in Chelonians, are well developed, jointed, and movable, and as a rule, articulate ventrally with the sternum. Contraction of the intercostal muscles drawing forward and straightening the ribs expands the thoracic cavity and the air rushes into the lungs through the open glottis. Relaxation of these muscles and descent of the ribs causes reduction in the size of the thoracic cavity and the expiration takes place. The process is further aided by the development of septa, which are modified diaphragms. These principles of respiration are the same for all Amniota except turtles, whose ribs are attached to the upper shell. Respiration in turtles is carried on by respiratory muscles located in the trunk.

ORDER RHYNCHOCEPHALIA*

The first order of reptiles, Rhynchocephalia, is represented by a single species, whose only living representative is Sphenodon or Hatteria (Fig. 40). It is a lizard-like reptile about 16 inches long, now confined to a few small islands off the coast of New Zealand. In its native habitat it is commonly called tuatara, a name that signifies the presence of spines which are found on the mid-dorsal line, at more or less regular intervals, from the head to the end of the tail. It is facing extinction, being eliminated by wild pigs, dogs and cats, reptile-eating tribes, brush fires, and civilization in general. There are no recent studies of the Sphenodon available.

These animals grow very slowly, so that full grown specimens are many years old. They are sluggish in habits and fond of the water, often lying full length in it during the greater part of the day. They may live in holes dug by the mutton bird but also burrow others for themselves in the loose sand and pebbles on the banks of rivers or islets. Captive tuataras are constantly burrowing.

Lung structure

The tuatara represents the simplest lung condition among reptiles. The lungs are two long thin sacs lined with infundibula throughout (Fig.41). They have partly transparent walls,

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*Entirely from A.K. Newman, 1877. This is the only account of any length.

on the inner surface of which are a few villous-like projections. The lungs extend nearly the whole length of the body. The left and right lungs are of nearly the same capacity, each with a large atrium. They resemble amphibian rather than reptilian lungs, but are efficient enough for an animal that is very sluggish, sleeps most of the day, and always moves slowly.

Air-tubes

The trachea is long and straight with soft, flexible rings of cartilage, irregularly arranged and incomplete on the dorsal side. The two bronchi are very short and terminate immediately after their entrance into the lungs.

Nostrils

The nostrils are two small holes almost hidden by lateral cranial skin ridges. A probe passed into them passes downward and forward.

Division of body cavity

The body cavity is not divided by a diaphragm, but a portion of the peritoneum is attached to the ribs where a diaphragm would be expected.

Mechanics of breathing

As the abdomen and thorax are tightly bound by the abdominal ribs, they do not change their form, and only the vertebral

ribs move during respiration. When the tuatara inspires its throat swells, then the lungs expand. The walls of the trunk are then motionless for many seconds, sometimes about half a minute before expiration occurs. The pharyngeal cavity is large and during inspiration it greatly depresses the hyoid and trachea, thereby enlarging the pharyngeal cavity still more. In this way, the animal inhales a large quantity of air, filling the lungs, trachea, pharyngeal cavity, and mouth, enabling it to remain under water for hours without coming to the surface. The quantity of air in all these cavities amounts to several cubic inches, which is sufficient to sustain life for some time in a small and cold-blooded reptile.

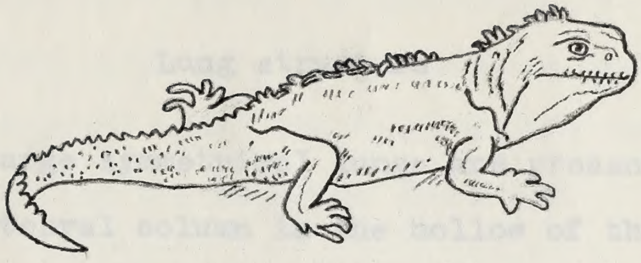

Fig. 40.—Sphenodon punctatum. (From Newman.)

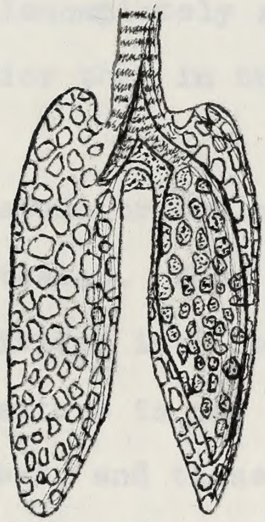

Fig. 41.—Lungs of Sphenodon, ventral view. Left lung opened to show the alveoli. (From Kingsley.)

ORDER CHELONIA (TURTLES AND TORTOISES)

Lung structure

Two very large symmetrical lungs are present, one on each side of the vertebral column in the hollow of the carapace. The parenchyma is well developed so the whole lung has a spongy texture. There is no atrium. The bronchus, on entering the lung continues as a large tube extending to the posterior end. From this main bronchial tube secondary bronchi diverge at right angles and end in incompletely separated air-cells which are smaller in the anterior than in the posterior portion of the lung (Fig. 42).

In the tortoise, Testudo orbicularis,* the lungs cover nearly the whole of the testae. They are cellular as in the frog. Each lung is subdivided into four or five indistinct lobules. The cellular texture is not uniform; the cells of the middle lobules are smallest, and those of the posterior lobule largest.

In Chelydra serpentina (Mitchell and Morehouse, 1863), the snapping turtle of the United States, the lungs are wedge shaped, with the base of the wedge located anteriorly. They lie in contact with the vault of the dorsal shield and are separated from each other by the large retractor muscles of the neck, the blood vessels, and the nerves. The walls of the lungs are very elastic, thus facilitating the act of respiration.

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*From Mitchell and Morehouse (1863)

They give no evidence of muscle fibers.

When the neck of a turtle is retracted, the trachea forms a loop to the left which is straightened out when the neck is extended. The bronchi enter the lungs at the ventral median edge, a little behind the anterior extremity.

Mechanics of respiration in Chelonia

Mitchell and Morehouse (1863), in a lengthy study, give their conclusions arrived at from numerous experiments to show the mechanics of respiration in the turtle. The function of the muscles was determined by observation, by stimulating them directly, and by irritating their nerves. The object of the report is to show that turtles do not swallow air in breathing but that their respiratory acts are carried on by inspiratory and expiratory muscles situated in the trunk. This explanation corrects a common idea that turtles inspire by swallowing air as frogs do. This idea probably arose from observation of the panting movements of the under part of the throat, common to both Amphibia and Reptilia.

The solid thorax prevents the freedom in respiratory movements that is typical of higher vertebrates. The ordinary quiet respiration in mammals, when the ribs are at rest and the cavity of the thorax enlarged by the descent of the diaphragm alone, is comparable to that of turtles in which the cavity is enlarged by the contraction of the muscles of the flanks.

Turtles breathe at very irregular intervals. These are much prolonged if the turtle is in water, and half an hour or more may elapse before it rises to the top to take two or three inspirations before plunging. Turtles breathe easily with the mouth open or shut, quite different from Amphibians. The respiratory process has three phases: (1) complete expiration; (2) complete and very full inspiration; (3) an appearance of slight or partial expiration followed by a pause of greater or less duration. This slight expiration relieves the lungs of any surplus air.

Whenever a turtle breathes in air, these triple actions occur, but when under water it occasionally expires air, without rising to the surface to renew the supply.

Mitchell and Morehouse found that the breathing power of turtles, unlike Amphibians does not lie in the hyoid arches, larynx, or mouth. In the turtle, the nostrils do not have valves as in frogs and the shape of the horny lips render it impossible to make the mouth air-tight enough to act as a chamber in pumping air into the lungs. Furthermore, the laryngeal cavity is too small to act as a chamber, and the hyoid arch in its descent does not enlarge the pharyngeal cavity.

The ability of turtles to hold air in the lungs at will, or when subjected to great external pressure as occurs in marine species, is determined by two pairs of muscles situated around the glottis and controlling its movements. These are the crico-

arytenoid muscle which opens the glottis lips and the crico-hyoid which acts as a sphincter, closing them. These muscles also prevent water from entering the lungs.

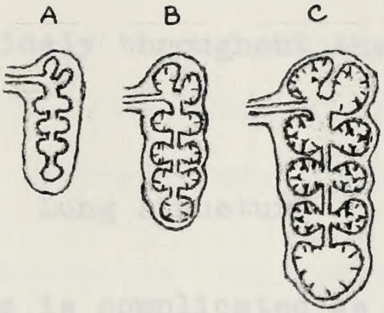


Fig. 42.—Diagram of formation of lungs in turtle.
View A, showing intrapulmonary bronchus, with several primary alveolar chambers invading the surrounding mesoderm.
View B, showing intermediate stage.
View C, showing the adult condition. The chambers have become subdivided into alveoli by ingrowths of their walls. The mesoderm has been reduced to partitions between the chambers. (From Walter.)

ORDER CROCODILIA

Crocodilia include the crocodiles, alligators, and caymans. They are distributed widely throughout the tropics and generally are enemies of man.

Lung structure

The lung structure is complicated as shown by the great increase in respiratory surface. The lungs are oval in shape (Fig. 81). The parenchyma is well developed giving the whole lung a spongy texture. There is no atrium. The main bronchus extends to the posterior end of the lung and branches systematically into secondary and tertiary bronchi, which divide into smaller tubes leading to infundibula (Cam. Nat. Hist. Vol. 8).

The lungs are enclosed in a pleural cavity, distinct from the abdominal cavity, due to the presence of partitions or so-called diaphragms.

Crocodilia is the first group of reptiles to have features that characterize it as a mammalian type of lung.

ORDER SQUAMATA

The two subdivisions of Squamata, the Lacertilia and Ophidia, comprise the most dominant group of reptiles of the present day. They exhibit a high degree of adaptation, being terrestrial, fossorial, arboreal, amphibious, and aquatic.

A. Lacertilia (Lizards)

There are 2500 living species. Although they prefer the tropics and subtropics, their representatives are found on cold Siberian plains, scorching deserts, moist lowlands, high mountains, and the seashore. They climb, run, swim, and burrow. The majority have well developed legs although a few degenerate burrowing forms are limbless as well as practically blind. Most of them are beneficial to man due to their preference for insect food.

Lung structure

The lungs are elongated sacs extending far back in the body cavity, usually paired but not always symmetrical (Fig. 44). The whole lung has a spongy texture with the parenchyma much better developed in the anterior region near the entrance of the bronchus, and gradually dwindling toward the apex which may be thin and saccular.

In lizards septa extend from the wall of the lung nearly to the bronchus (Fig. 38), thus dividing the lung into chambers that

are lined with alveoli (Fig. 45). Each septum consists of a central framework of elastic fibrous tissue lined on either side by a network of capillaries. This plexus is covered by hyaline pavement epithelium. Tracts of ciliated epithelium are found along the margins of the cells, the course of the blood vessels, and along the denser tissues. The double layer of blood vessels in each septum is a point of structure characteristic of the reptilian lung. (Williams, 1859).

The Varanidae which surpass all modern lizards in size are the highest form of Lacertilia. The lung is spongy throughout, and has no atrium. The bronchus divides into distinct secondary bronchi which have smaller divisions that lead to infundibula.

In Ascalobatae, Iguanidae, and Varanidae (Goodrich, 1930) the terminal thin-walled sacs may be prolonged into blind processes. These are especially numerous in Chameleons where they extend among the abdominal viscera and help the animal to distend itself.

Camp's "Classification of Lizards" (1923) includes the following outline of lungs.

"Milani (1894) distinguishes four degrees of differentiation of the lung structure in lizards.

(1) Sphenodon type. This type is found in certain scincs and teiids. The lungs are simple alveolar-walled sacs without septa and different from Amphibia only in specialization of the trachea.

(2) Lacerta type. Here there are a number of septa dividing a portion of the lungs into small internal chambers. This type is developed from the Sphenodon type by enlargement of some of the alveolar walls and is not essentially different from it. This type is found in

a. Gekko verticillatus
b. Gekko vittatus
c. Tarentola mauritanica
d. Tarentola annularis
e. Gymnodactylus platurus
f. Thecadactylus rapicauda
g. Hemidactylus turcicus
h. Calotes jubatus
i. Tiliqua
j. Lacerta ocellata
k. Lacerta agilis
l. Lacerta viridis
m. Zonurus giganteus

(3) Iguana type. This type is found in a number of iguanids and agamids. The lungs of Heloderma and Phrynosoma approach but do not attain the typical development of this type. It is still more highly specialized by marked extension and enlargement of the less numerous septa.

(4) Varanus type. This is the most highly modified of all with long internal bronchi and a spongy internal reticular net-

work as in mammals. The 'avian lungs' of Uroplates and Polychrus have the finger-like processes characteristic of some chameleons. Internal septa develop as in the iguana type."

California Limbless Lizard—Anniella pulchra

Coe and Kunkel (1906) made a detailed study of Anniella pulchra, a limbless lizard widely distributed in California, Arizona, and southward. It prefers dry and barren localities, deserts, and the sand dunes of the seashore. This lizard is of interest because it presents a number of anatomical features which deviate more or less from those characteristic of lizards. Both lungs are functional. The right lung is much elongated and well developed while the left is small and rudimentary. Both have a similar anterior lobe.

The larger right lung is long and tubular (Fig. 46), largest in its middle portion and tapering gradually to a slender pointed posterior end. The trachea enters the median border of the lung a short distance behind the anterior end, which is thus extended forward as a short lobe. The lumen of this lobe is directly continuous posteriorly with that of the main portion of the lung, although there is often a slight constriction in this region. If the constriction is marked, the opening into the posterior end of the lobe is narrow.

The left lung is usually less than ¼ as long as the right. The cavities of the two lungs are connected by a narrow opening,

oval in outline, and situated at the extreme posterior end of the trachea. The anterior projection from the rudimentary left lung is often as large as the corresponding projection in the right lung.

Although the cavities of the two lungs are well separated, the lungs themselves are closely bound together by a sheath of strong connective tissue except at their anterior and posterior extremities.

Both lungs are functional throughout in spite of the great difference in size. Their walls are thin and membranous as the septa bearing the blood vessels form only shallow alveoli. The atrium, therefore, is nearly as large as the lung itself.

The large lung occupies the right side of the body cavity and extends posteriorly on the dorsal side of the liver, while the esophagus occupies a corresponding position on the left side of the body. When the esophagus is empty and the lung distended, the latter actually fills the whole ventral portion of the body cavity for some distance behind the heart and then lies ventral to the esophagus.

In an adult lizard, about 170 mm. long, the average length of the right lobe is about 35 mm. and that of the left lobe about 8 mm. The length of the trachea is about 30 mm. There is great variation is size, particularly in regard to the rudimentary lung.

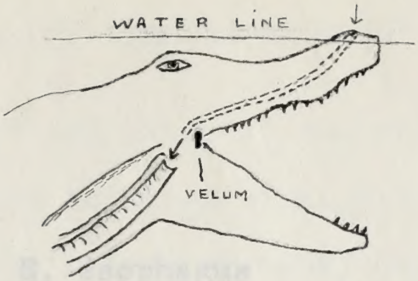


Fig. 43.—Diagram to show the choana (dotted) in alligator. It leads to trachea behind a flap-like velum in the back part of mouth cavity, which enables the animal to breathe under water and at the same time to drown its prey held between the jaws, so long as external nostrils are above the water line. The velum closes off the inner choanal opening from the mouth cavity. (From Walter.)

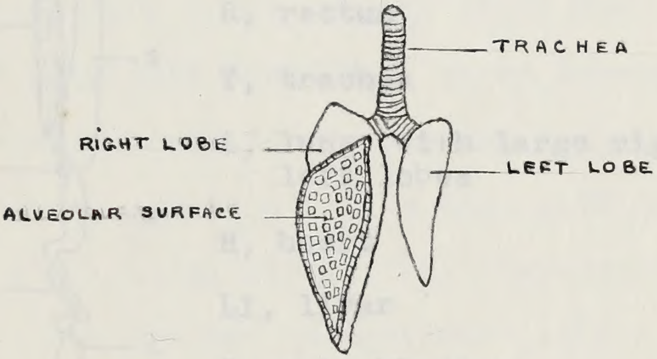


Fig. 44.—Lungs of the lizard, Sceloporus. (From Adams.)

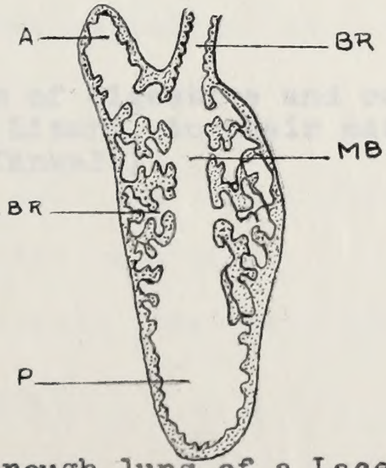
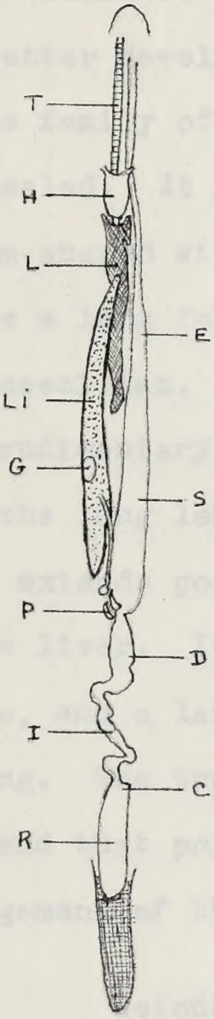


Fig. 45.—Section through lung of a Lacertilian. BR, lateral external bronchus; MBR, main internal bronchus; LBR, secondary bronchus leading to air-cells; A, anterior saccular extensions of bronchi; P, posterior extensions of bronchi. (From Goodrich.)



E, esophagus

S, stomach

D, duodenum

I, ileum

C, rudimentary caecum

R, rectum

T, trachea

L, lung, with large right, and rudimentary left lobes

H, heart

LI, liver

G, gall bladder

P, the lobes of pancreas and spleen

Fig. 46.—Diagram of digestive and respiratory organs of California Limbless Lizard, in their natural positions, ventral view. (From Coe & Kunkel.)

Amphisbaena Braziliana*

This lizard is the exception to the rule that the right lung is better developed in cases of asymetry. It belongs to a degenerate family of the burrowing type, legless, with eyes and ears concealed. It greatly resembles the Amphibian caecilian, being worm-shaped with numerous rings formed by the soft skin but it has a long forked tongue by which it may be distinguished from the caecilian.

The rudimentary right lung is about one-half inch long, and like the long left lung has a short forward extension. The left lung extends posteriorly into the body cavity as far as the end of the liver. It is a simple sac, with the usual honey-comb appearance, and a large atrium, all characteristic of the typical lizard lung. The trachea is continued only a short distance into the lung and that portion within the lung shows irregularity in the arrangement of the rings of cartilage.

Heloderma suspectum (Gila monster)**

This lizard is the only poisonous lizard native to the United States. It is called a beaded lizard because the body is covered with bead-like tubercles.

Unlike the two lizards previously discussed, Heloderma

*From Beddard (1905)

**From Shufeldt (1890)

suspectum has large symmetrical lungs (Fig. 47). They are wide anteriorly and narrow gradually, ending in a rounded tip. In the anterior part the tissue is fine and spongy, while the posterior region is composed of sacs covered by a serous coat of dense texture, filled in by air-cells that are larger and more open. This is a typical condition in this class of vertebrates.

The glottis is a narrow, medio-vertical slit with no epiglottis, but the sides press close together so food is prevented from entering the trachea. The trachea, including the larynx was 7½ cm. long in this specimen, and composed of about 57 cartilaginous rings, all incomplete dorsally. A few of these bifurcate as in man. Throughout their length the bronchi are almost as wide as the trachea. They curve slightly in the anterior part of the lung. Cartilaginous rings are lacking posteriorly where the lung tissue is coarser. Bronchial branches are not definite as communication is made with the lung by means of short necked apertures found at a few points along their sides, mostly anteriorly.

Chameleons

Certain lizards, notably chameleons, have lungs with sac-like extensions (Fig. 48) which enable them to swell up to some extent, an act which is more of a protection than a respiratory aid (Walter, 1928). In most other respects the chameleon lung is a typical Lacertilian lung with a large atrium, lung tissue

more compact and spongy in the anterior part than posteriorly where the terminal sacs are thin-walled and less vascular. The long thin-walled processes extend among the viscera where-ever there is room. Their form may be spindle or club shaped or lobulated.

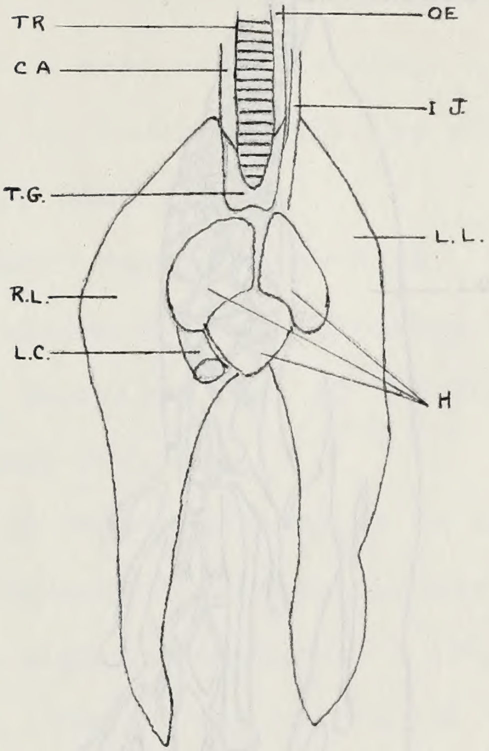


Fig. 47.—Anatomy of Heloderma suspectum, ventral view.

TR, trachea

C.A., carotid artery

T.G., thyroid gland

R.L., right lung

L.L., left lung

L.C., anterior cap of peritoneum (cut short) in which the lobulus cardiacus of liver is lodged

OE, oesophagus

I.J., internal jugular

H, heart

(From Shufeldt.)

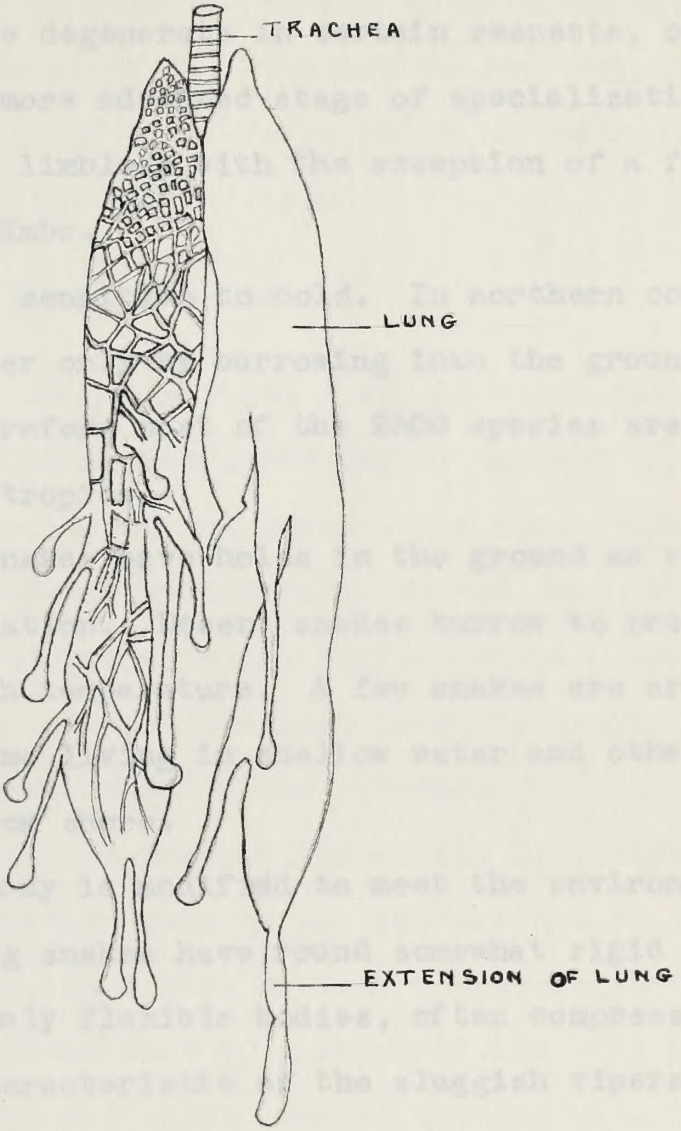


Fig. 48.—Lungs of Chamaeleo monachus. (From Wiedersheim.)

B. Ophidia (Snakes)

Although snakes are degenerate in certain respects, on the whole they represent a more advanced stage of specialization than lizards. They are limbless with the exception of a few that have rudimentary limbs.

They are extremely sensitive to cold. In northern countries snakes survive the winter only by burrowing into the ground below the frost line, therefore most of the 2300 species are found in the tropics or semi-tropics.

General types of snakes have holes in the ground as retreats in danger or for hibernation. Desert snakes burrow to protect themselves from the high temperature. A few snakes are arboreal. Several are aquatic, some living in shallow water and others in deep ocean water far from shore.

The shape of the body is modified to meet the environmental requirements. Burrowing snakes have round somewhat rigid bodies. Tree snakes have extremely flexible bodies, often compressed. Flattened bodies are characteristic of the sluggish vipers and many desert-dwelling forms. Some aquatic snakes are short and heavy but others are slender with the posterior part of the body compressed.

The sternum is lacking and snakes actually walk on their ribs, each of which is equipped with a separate muscle. The ribs of snakes are attached dorsally along the entire length of

the backbone which is made up of numerous vertebrae. The articulations of the vertebrae give the snakes their litheness, so that with a single movement of the ribs and scales they can climb, leap, swim, and stand erect for a third of their length, and run swiftly without the aid of legs.

Lung structure

In the snake there is, as a rule, a single elongated lung, the right. The left is rudimentary and may or may not be functional. Sometimes it is absent altogether. In some species both lungs are almost equally well developed, but the left is generally shorter. In addition to the typical lungs, some snakes have a structure called a tracheal lung, formed by respiratory tissue at the dorsal side of the trachea.

The rudimentary lung, if present, is on the left side of the body but in a few species this is not evident due to displacement of the viscera, in a more or less rotary direction. Butler (1895) has determined that in snakes, if one lung is rudimentary, it is always the left. One of the characteristic displacements is of the larger right lung from the right side into a dorsal position underlying the vertebral column and extending partly into the left half of the body. Therefore, the right lung is in the various accounts of Cope referred to as the dorsal lung, and the left, if present, as the ventral lung.

The lung is perfectly smooth externally and with few exceptions internally for the posterior two-thirds of its length (Fig. 81). The inner surface of the anterior third becomes more and more divided until the anterior sixth where it is elaborated into many small sacs or alveoli, each of which communicates by a circular opening with the cavity of the lung (Miller, 1893).

Each alveolus (Williams, 1859) divides into secondary and tertiary alveoli. The individual air-cells are surrounded by a septum that is complete, so there is no communication between the cells. This septum has two layers of capillaries separated from each other by an intermediate layer of elastic tissue. Over the interior of the lung ciliated epithelium is distributed sparsely along the courses of the larger blood vessels, the borders of the cells, and along the lines of thickened tissue.

Python (Cuvier)

The Python is described by Hopkinson and Pancoast (1837) and serves as an example of a snake that has two well developed lungs. The Boas which belong to the same family as the Pythons have the same fundamental structure. "The only serpents in which there is a pair of well-developed lungs are the Boidae" (Beddard, 1906, Vol. 1). No tracheal lung is present in either (Cope, 1894).

In this specimen of Python (Cuvier) the trachea is 1' 8" long and 3/8" wide, with cartilaginous rings incomplete dorsally. Each ring is connected to the adjoining one by an elastic membrane, so that when the trachea is stretched lengthwise, it easily regains its former condition. In the region of the heart, the trachea divides into two bronchi.

The lungs are two distinct bags, united along their middle edges but separated at their ends. The difference in size is less marked than in most snakes. The right lung is 2' 10" long and about 4" wide, and extends as far as the gall-bladder. The left lung is 1' 9" long and 3" wide, and extends as far as the posterior end of the liver.

The upper part of each lung is spongy, the parietes thick, and the inner surface covered with a loose reticulated tissue. The lower 4/5 of each lung is thin, semi-transparent, and has fewer blood vessels than the upper part.

Pelagic Serpents

Hydrophis schistosa*

Pelagic serpents (Cantor, 1841) compared with terrestrial serpents show great modification in structure especially of the respiratory system. In all other serpents, the anterior ribs only are used in respiration but in the pelagic serpent whose lung extends to the anus, the entire set of ribs assists in respiration. In a specimen of Hydrophis schistosa three feet,

*From Cantor (1841)

ten inches long, Cantor counted 168 ribs. A tracheal lung is present (Cope, 1894).

The nostrils are small and furnished with a membranous valve which is open to admit air and closed to prevent the entrance of water.

The trachea is long and cylindrical and gradually widens posteriorly. It extends as far back as the liver. At some distances anterior to the heart it becomes cellular and from this point the single lung commenced (Fig. 50). The lung is long, narrow, and cylindrical but in several places it widens into spacious sacs (Fig. 49). Near the posterior end of the liver it becomes narrow and continues so for the rest of its length. It is attached by a short round ligament near the anus.

Internally the lung structure is unusual because the entire lung is spongy, although to less degree in the posterior part. The whole of the cavity of the lung is lined with cilia.

This great development of the lung indicates the importance of its functions. First, it serves as an organ of respiration and a reservoir for air, which allows oxidation to be carried on in the body for a considerable length of time when the mouth and nostrils are closed, while the serpent goes to great depths in search of food.

Secondly, the lung filled with air floats the body, particularly when food is swallowed and the specific gravity is increased. The filled stomach, by pressing against the lung

causes the part posterior to it to become isolated and serve as a float.

Tracheal lungs

In snakes "the lung-substance may exist from the very commencement of the trachea, forming the so-called 'tracheal lung' which itself shows considerable variation in its condition in different serpents." (Beddard, 1906).

In discussing the wide distribution of the tracheal lung, Beddard, referring to Cope says "...after a survey of the leading groups of Ophidians found it to occur in the principal subdivisions of the order or suborder."

Thompson (1913) gives some reasons for the presence of tracheal lungs. (1) The tracheal membrane contributes to the flexibility of the trachea, permitting it to be subject to greater pressure especially when bulky morsels pass through the esophagus. (2) Being continuous with the lung, it increases the pulmonary area, especially when the lung has been encroached upon by other organs, as in Viperidae, where the elaboration of venom requires a large liver. Since the body in these serpents is, as a rule, short and thick, the liver crowds the lung, so the pulmonary tissue tends to spread out along the tracheal membrane. (3) In Hydrophidae, sea-going snakes, an increase in pulmonary area is required to give buoyancy and to enable the snakes to remain for some time beneath the surface. In

Acrochordinae, the members of which are aquatic in their habits, there is a highly developed tracheal lung.

Cope (1894) found marked gradations in the tracheal lung. In the genus Heterodon (puff-adder) it exists as a pocket along the trachea, reaching to the head, and without communication with the trachea except by way of the lung. In Solenoglypha (vipers), without exception, the tracheal lung exists, extends to the head, and its lumen is continuous with the trachea and with the normal lung. This is true also of the sea-snakes in in the genera Hydrus and Hydrophis, and in genus Ungualia, the only one in Peropoda to have a tracheal lung. The tracheal lung is distinct from the true lung in Platurus and Chersydrus (sea-snakes). In Platurus the trachea is separate from the lumen of the tracheal lung while in Chersydrus it is not.

The Hamadryad snake (Ophiophagus bungaris) or King Cobra (Beddard, 1903) shows a peculiar structure in the trachea and tracheal lung. The dorsal tracheal membrane is perforated throughout most of its length by 26 or 27 oval openings, regularly spaced (Fig. 51), and leading into chambers which do not communicate with each other nor with the lung. Between these openings are rounded thinnings of the tracheal membrane. Beddard interprets these chambers as possible remains of the tracheal lung, in which the respiratory function has been lost.

In Coluber corais (Beddard, 1906) the tracheal lung is developed to a great extent but as an air-sac rather than a

respiratory organ. Almost from its beginning the trachea ceases to be a closed tube and opens out into a gutter. The free ends of the cartilaginous rings are connected by a thin-walled sac several times the diameter of the trachea itself. This sac is honeycombed and vascular in such a small area that it can aid very little in respiration.

In Erythrolamprus aesculapii (Beddard, 1906) the tracheal lung (Fig.53) is very small, but functional. It is honeycombed and vascular like the lung, and continuous with it.

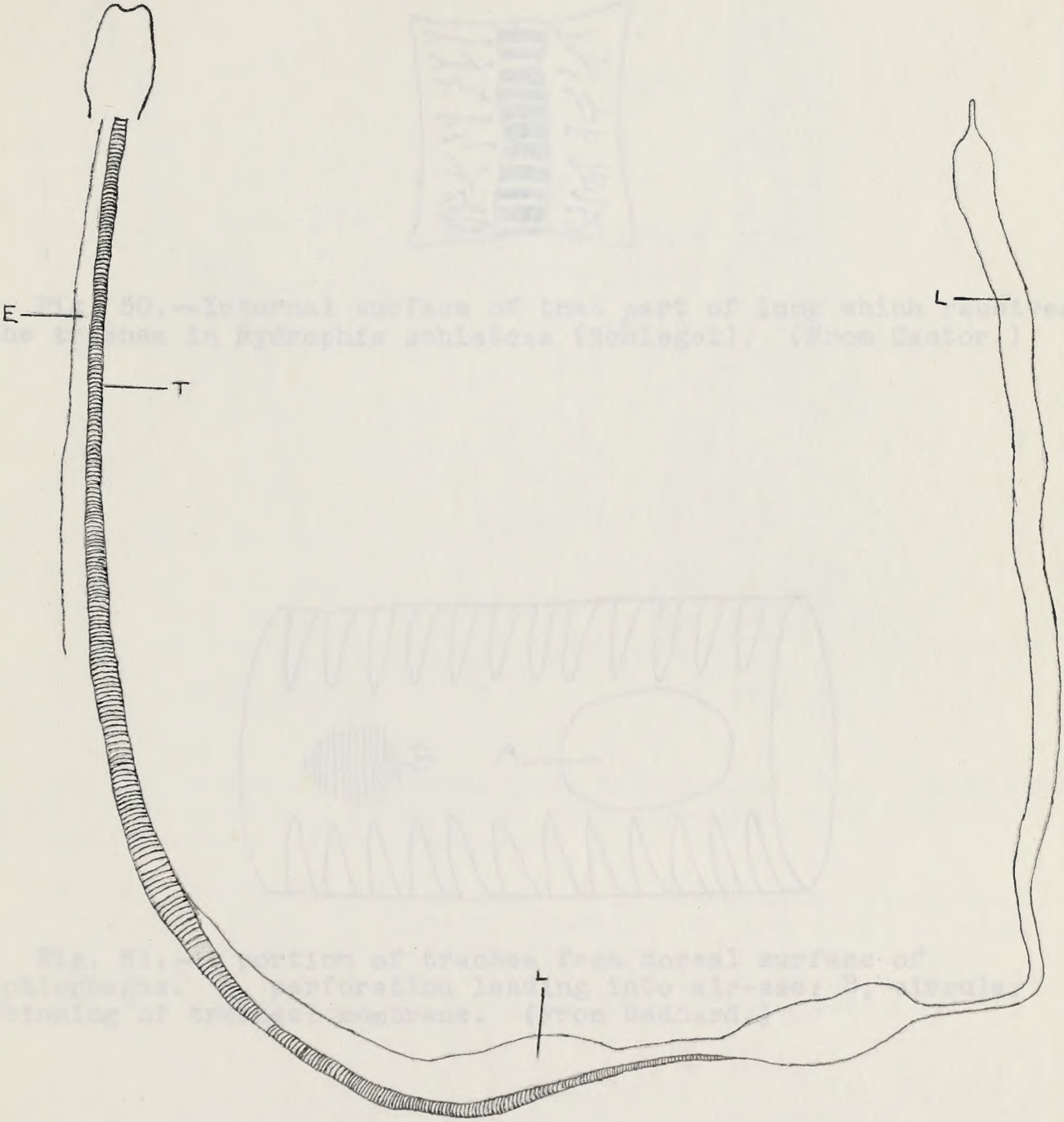


Fig. 49—Dissection of young pelagic serpent, Hydrophis schistosa (Schlegel). E, esophagus; T, trachea; L, lung. Total length of trachea and lung is 3' 2". (From Cantor.)

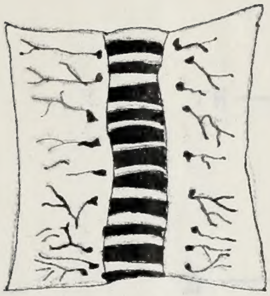


Fig. 50.—Internal surface of that part of lung which receives the trachea in Hydrophis schistosa (Schlegel). (From Cantor.)

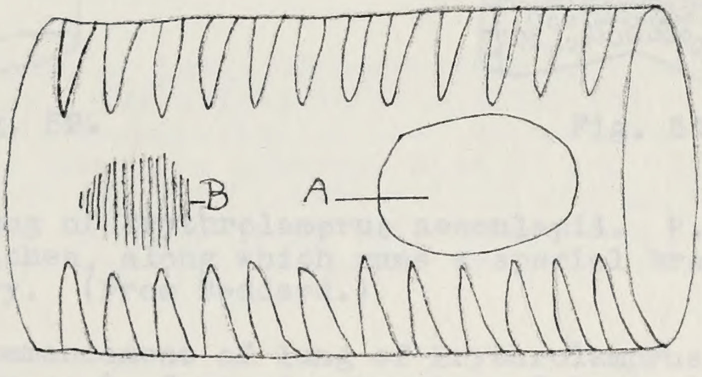


Fig. 51.—A portion of trachea from dorsal surface of Ophiophagus. A, perforation leading into air-sac; B, circular thinning of tracheal membrane. (From Beddard.)

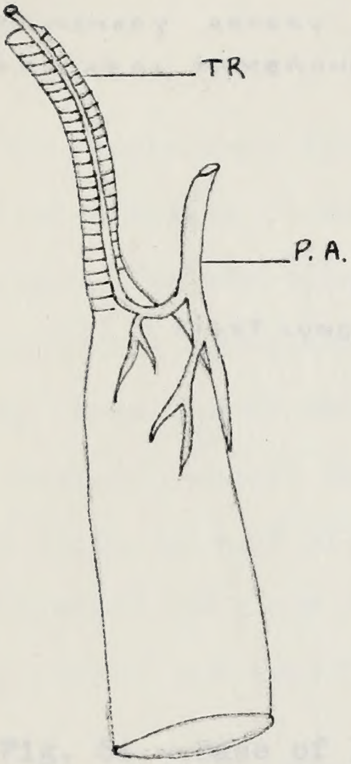


Fig. 52.

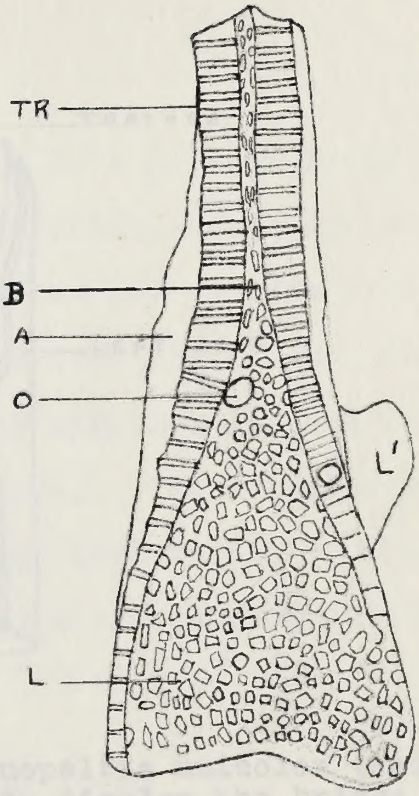


Fig. 53.

Fig. 52.—Lung of Erythrolamprus aesculapii. P.A., pulmonary artery; TR, trachea, along which runs a special branch of the pulmonary artery. (From Beddard.)

Fig. 53.--Commencement of lung of Erythrolamprus aesculapii, cut open. L, lung; A, forward extension of lung along trachea; O, orifice of headward extension of lung (A) into main lung. L', rudimentary second lung, the orifice into which is shown in the tracheal semirings; B, tracheal lung. (From Beddard.)

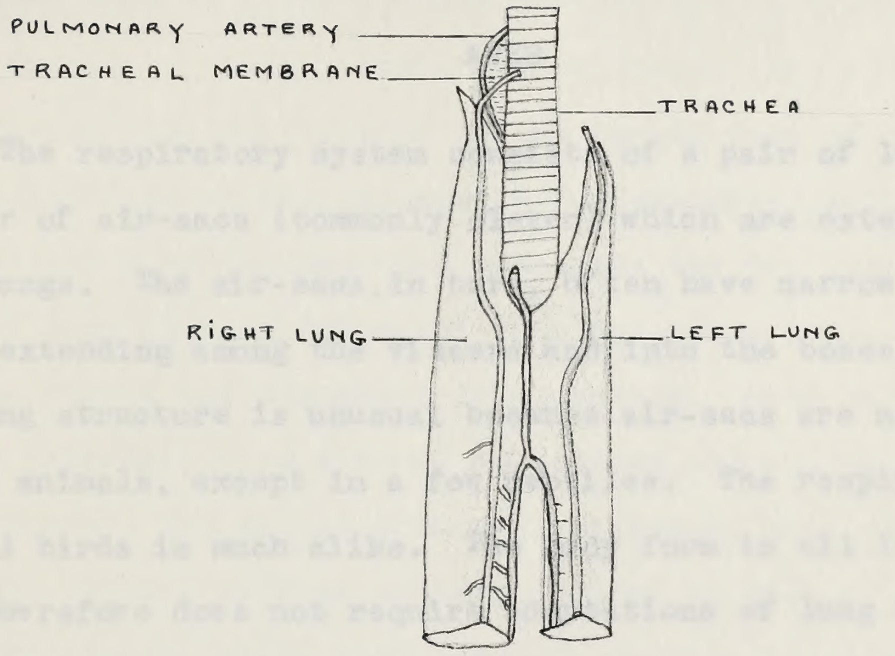


Fig. 54.--Base of lungs of Xenopeltis unicolor (Reinhardt), viewed from below. The object is to display the bridge uniting the two lungs, the termination of the trachea, the long free apex of the left lung, the adherent apex of the right lung, with its tiny free tip, and anterior to it the portion of the tracheal membrane which is lined internally with pulmonary tissue and is bordered by a branch of the pulmonary artery. (From Thompson.)

AVES

The respiratory system consists of a pair of lungs and a number of air-sacs (commonly eleven) which are extensions of the lungs. The air-sacs, in turn, often have narrow elongated sacs extending among the viscera and into the bones. This type of lung structure is unusual because air-sacs are not found in other animals, except in a few reptiles. The respiratory system in all birds is much alike. The body form in all is similar and therefore does not require adaptations of lung structure as do amphibians and reptiles.

Structure of the lungs

The lungs are small in comparison to the size of the bird. They extend (Williams, 1859) from the second dorsal vertebra as far as the kidneys and laterally to the junction of the vertebral ribs with the sternal ribs. They are symmetrical, flattened, and irregularly triangular in shape. They are held firmly between the skeleton on the dorsal side and an almost rigid sheet of connective tissue, the pulmonary diaphragm or aponeurosis on the ventral side. They are fixed by areolar tissue to the ribs and vertebral column and bear a deep imprint of these bones. They are capable of very little distension and undergo

less change in shape than lungs of other groups, especially mammals, where the lungs lie free in the thoracic cavity.

Each lung is a three-sided pyramid with a posterior base, and a dorsal, a medial, and a ventral face. The ribs lie in deep furrow-like depressions in the dorsal face of the lung. The medial face of the pyramid is the smallest, and is in contact with the mediastinum that separates the two lungs. The ventral face is more irregular than the other two. Its anterior part is convex and posterior part concave. Both parts, especially the anterior, have a rough appearance and are marked with deep furrows, due to the bronchial branches, many of which lie near the ventral surface and are covered by only a thin membraneous pleura, which when removed, reveals the rough appearance of the lung and the openings leading to the air-sacs. (Muller, 1907).

The respiration of birds even when at rest is more active than that of mammals. If the lungs were constructed after the mammalian type, they would need to be very large, and powerful respiratory muscles would be required. This would add to the weight of the body. The lungs, therefore, are very porous and light in weight, more fragile than the lungs of mammals, but highly vascular, being bright red in color, with the blood more freely exposed to the air.

The lung is spongy but has little elasticity (Headley, 1895). The tissue consists of numerous septa with a complex

network of interlacing blood capillaries and air capillaries (Goodrich, 1930). The air-cells are hexagonal areas surrounding the parabronchi. The air in the minute air-tubes passes close to the blood.

The respiratory epithelium of birds has been studied by various investigators with the conclusion by many that the capillaries of the finest air-passages are uncovered. This belief is held by Rainey (1849) who states that since there is no epithelial layer in the individual air-cells aeration takes place without the necessity of either ciliated epithelium or basement membrane, and simply by the action of the inspired air upon the blood in the capillaries, with no other membrane intervening but the capillary wall. He also believes that the capillaries interlace enough to hold them together so air is allowed to pass freely between and all around them.

Concerning these findings, Ogawa (1920) makes the following comments: "...from histological evidence it seems reasonable to conclude that no respiratory epithelium is present in the respiratory spaces of birds."

Many authors "are of the opinion that the respiratory epithelium of birds, though not actually demonstrated, must be present."

"If the respiratory spaces of birds were bare, it would be the only case in higher animals in which either an external or an internal surface of the body has no coating of epithelium."

"The fact that no analogous case has been found in which the epithelial coating of a free surface is lacking has led Oppel and other authorities to conclude that the lung of the bird must have respiratory epithelium in spite of the absence of actual confirmation."

Air-tubes

The trachea is generally a straight tube passing into the thorax where it divides into two bronchi. Sometimes, however, it is greatly elongated to varying degrees by turns or loops similar to those found in crocodiles and turtles.

The trachea is composed throughout of rings which are cartilaginous or may be wholly or partially ossified. The rings are generally simple and alike, incomplete, or complete except at the bifurcation of the trachea where they are modified in connection with the formation of the syrinx. (Beddard, 1898).

Each bronchus enters the mid-ventral surface of the lung (Fig. 57) and immediately expands into a vestibule. It then narrows and continues as a main trunk, the mesobronchus, along the ventral side of the lung and ends in the abdominal air-sac.

Within the lung, the mesobronchus retains its cartilaginous character for some distance although rings are notpresent in its walls (Müller, 1907).

In contrast to mammals where the bronchial tubes pass directly to the central part of the lung before sending branches

to the periphery, in birds they pass toward the periphery first and then send branches toward the center (Ross, 1898).

The mesobronchus gives off secondary bronchi (Fig. 57). As a rule (Goodrich, 1930), there are four large secondary ventral bronchi, called entobronchi, which supply air to the lung; eight secondary dorsal bronchi, called ectobronchi, which supply air to the air-sacs; six laterobronchi and a number of dorsobronchi. The entobronchi and ectobronchi give off tertiary bronchi called parabronchi that are so numerous that the orifices leading to them give the entobronchi and ectobronchi a sieve-like appearance (Müller, 1907). The parabronchi correspond to the bronchioles of mammals. They bear a number of elongated diverticula, radially arranged (Fig. 58). The angles at which the parabronchi leave the secondary bronchi are always close to a right angle. They are often arranged in one or two rows, or spirally (Müller, 1907). They often anastomose with those of neighboring bronchi and of the recurrent bronchi. (Goodrich,1930).

Some parabronchi send blind tubes into the interior of the lung which meet but do not communicate with those from the opposite side. At points where two or more parabronchi meet there are large openings which communicate with the air-sacs, bones, etc. Fig. 81 (Miller, 1893).

The recurrent bronchi are explained by Goodrich (1930) as follows: Each of the air-sacs, except the cervical, has, as a rule, "...a group of small secondary openings leading back

from the sac into recurrent bronchi which penetrate and branch in the substance of the lung; and it is by means of these that relatively pure air received directly from the primary bronchus is returned to the lung from the sac, ensuring a thorough ventilation of the parenchyma. ...The mechanics regulating the flow of air from the sac back to the lung through the recurrent openings and not through the ostia has not yet been satisfactorily elucidated."

Air-sacs

The air-sacs may be described as the blown-out extremities of certain bronchial tubes. The number varies slightly as do the names given them by different authors. The list taken from Goodrich (1930) is as follows:

1. Cervical air-sacs. Paired. Extending along the neck.
2. Interclavicular air-sacs. Usually fused to form a median sac ventral to the esophagus in the pectoral region.
3. Anterior intermediate air-sacs. Paired.
4. Posterior intermediate air-sacs. Paired. The two pairs of intermediate air-sacs are located below the ribs and anterior to the post-hepatic septum.
5. Abdominal air-sacs. Paired. Found in all birds except Apteryx. This is the only pair in the abdominal cavity.

An additional pair, the axillary air-sacs, is given off from the cervical air-sacs.

A few examples from Beddard (1898) will serve to show the variation in air-sacs. In storks the praebronchial (cervical) break up into at least five, and the two subbronchial (interclavicular) completely fuse into one. In Chauna there is even greater division of the praebronchials. In Podargus there are three instead of two pairs of intermediate air-sacs. In Accipitres the abdominal air-sacs are peculiar in that one of the walls of the sacs is firmly attached to the ventral parietes and the walls of the two sacs enclose between them the intestines which give the appearance of being enclosed in a special compartment of the coelom. In one or two Accipitres there are three intermediate air-sacs.

The interclavicular air-sacs do not fuse in Vultures, Ciconia, Ardea (Goodrich, 1930).

Apteryx, the New Zealand flightless bird, is the only bird whose air-sacs are confined to the thoracic cavity (Figs. 59 & 60). Owen (1841) mentions but four air-sacs on each side, an anterior and three inferior sacs. Huxley (1882) considers this an error and names five; a praebronchial (cervical), a subbronchial (interclavicular), an anterior-intermediate, a posterior intermediate, and a posterior. The latter pair which is called the abdominal by some authors (Beddard, 1898; Wiedersheim, 1897) is small in apteryx and completely enclosed by the oblique

septum so does not extend into the abdominal cavity among the viscera (Wiedersheim, 1897). The air-sacs are much reduced and do not send extensions into the bones (Walter, 1928).

Air-sacs communicate with the lungs by five orifices on the ventral surface of each lung. There is one orifice to each sac, except the unpaired sac which has two, one from each lung (Ross, 1898).

Authorities vary on the question whether or not the air-sacs communicate with each other. Headley (1893) states that if the trachea of a dead bird is tied, and air blown through a break in the humerus all the air-sacs will expand as completely as though air were blown into the trachea. This would indicate that they do connect with one another.

Each air-sac consists of a main sac from which numerous diverticula arise. The latter possess many secondary diverticula (Müller, 1907).

In addition to the regular air-sacs other spaces of a different nature occur, such as the tracheal labyrinths of ducks and emus (Gadow, 1890) and the pneumatic cavities of the bones of the head. The skull is aerated by a set of spaces which are not connected with the breathing system, but with the Eustachian tubes and the nasal chambers (Beddard, 1898).

The tracheal labyrinth in the emu is a peculiar structure closely resembling the tracheal lung of the type found in the snake Ophiophagus, except in the emu it is present on the ventral side. There is a slit on the trachea where the rings

do not meet in the mid-line. It leads into a thin-walled outgrowth of the lining of the trachea and is divided into two by a septum. However, there is no evidence of any connection between this tracheal pouch and the lung.

Structure of the air-sacs

The air-sacs are formed by a dilation of the mucous membrane of certain bronchial tubes. They are thin-walled non-vascular sacs that become pressed against each other and against the ventral surface of the lung, and the oblique septum. They are permanently distended with air to a greater or less extent (Goodrich, 1930). Ross (1898) did experiments on chickens to study air-sacs and found them to be transparent membranes with more or less fibrous connective tissue basement. When inflated they are easily destroyed. The following points are brought out by Ross in regard to the structure of the epithelium. (1) The epithelium is pavement in any portion of the air-sacs not attached to the walls of the body. (2) The epithelium near the bronchial tubes is columnar, and gradually changes to pavement epithelium. (3) In a two or three day old chick the cells are pentangular with round nuclei (Fig. 63). If examined while fresh they appear granular with cilia in motion. (4) Where the sacs are attached to the surrounding tissue the epithelium varies greatly, showing pavement, cuboidal, and columnar cells, all in the same section (Figs. 64, 65, 66). Cilia are present near the

connection of the sacs with the lungs, and also over the entire surface of the sacs. Fresh tissue from any part of the sacs exhibit rapidly moving cilia. No cilia were found in the axillary air-sacs (Fig. 62, Ax), in the abdominal air-sacs around the head of the femur (Fig 62, ABD), or in the cavities of the bones.

Functions of the air-sacs

Following is a list of the functions attributed to air-sacs by the numerous investigators who have studied them.

1. Although they aid in respiration in many ways they themselves do not have respiratory functions because their walls are not vascular, but supplied only sparsely with blood (Kingsley, 1912).

2. Their most important work is to aid in inspiration and expiration, (Droisier, 1866; Headley, 1893; Wiedersheim, 1897; Kingsley, 1912; Walter, 1928; Goodrich, 1930). Headley (1893) measured the cubic content of the lungs and air-sacs of a pigeon and found the capacity of the air-sacs to be five times greater (and probably more) than the capacity of the lungs. This extra amount of air would be of use in breathing. When a bird exhales, comparatively fresh air from the sacs is driven into the lungs, so that exhaling as well as inhaling renews the supply of oxygen. In inhaling, the body cavity is expanded, a vacuum created in the sacs, and air rushes into them.

Rainey (1849) estimated the size of the air-spaces between the capillaries to be 1/9600 of an inch. Consequently, the

oxygen in them is soon used, and the supply renewed by the continuous air supply that passes from one air-sac to another.

Again, during movement of the body, the air-sacs alternately expand and contract causing air to pass continually through the lung tissue. During flight, the interclavicular and anterior intermediate sacs would be most influenced by the muscles of the wings; at rest or walking the posterior intermediate and the abdominal sacs would be most active (Goodrich, 1930(. Thus, during flight the thoracic framework remains rigid as an attachment for muscles and at the same time air passes over the respiratory surface of the lungs to and from the air-sacs.

3. The body temperature varies from 100°F. to 112°F. It is regulated mainly by the lungs and their extensions. Increasing the rate of breathing is the chief means of keeping the temperature down. The expired air is about the same temperature as the body and the greater the amount of air breathed in and out in a given time, the more the body will be cooled (Headley, 1893).

The air-sacs are filled with warm moist air which helps to maintain the body temperature. In the absence of sweat glands, the skin of the bird is of little service in regulating body temperature. Since the air-sacs are located toward the outer surface of the body, they aid in heat regulation (Wiedersheim, 1897; Walter, 1928; Goodrich, 1930; Adams, 1933).

4. The arrangement of the air-sacs is such that a proper center of gravity is established for balanced flight, thus easily maintaining the equilibrium of the body (Kingsley, 1912; Walter, 1928).

Air-sacs, when inflated lessen the specific gravity materially. Without them it would require more muscular effort to sustain the body in air for considerable periods of time. Possibly their distended condition mechanically aids in maintaining the wings in an extended position during soaring or gliding to earth.

Long ago it was thought that air-sacs serve as aerostatic organs but Campana (Goodrich, 1930) proved that their lifting power is negligible. They may lower the specific gravity of a bird's body by 4% at the most.

In floating and diving birds, however, the air-cavities act as hydrostatic organs

5. The air-sacs enlarge the anterior part of the thoracic cavity, especially the part surrounded by the pectoral arch. A larger development of the skeleton can take place, giving an increase of surface for muscular attachment without much increase in weight (Wiedersheim, 1897).

6. The extensions of the air-sacs between the muscles lessen friction (Wiedersheim, 1897; Walter, 1928).

7. In singing birds they serve as reservoirs for air (Goodrich, 1930). During flight they also serve as reservoirs (Walter, 1928).

Extensions of air-sacs

In many cases, extensions from the air-sacs find their way into the bones as the marrow is absorbed (Headley, 1893). The pelvis, humerus, coracoid, sternum, and ribs are most frequently pneumatic, and the femur, furcula, and scapula less frequently (Kingsley, 1912). Extensions are found among the skin (Weysse, 1911), and muscles, especially in good fliers and aquatic birds (Goodrich, 1930). They supplant the connective and fatty tissue beneath the skin in pelicans (Walter, 1928). They may extend even into the feathers (Headley, 1895).

The fact that bones of birds often contain air instead of marrow is said (Goodrich, 1930) to have been first mentioned by Emperor Frederick II in a treatise on the chase in the thirteenth century. Various functions are attributed to pneumaticity of bones, but this condition is not directly connected with respiration.

Diaphragms

Birds possess numerous septa, two of which, at least, are commonly termed diaphragms, although in structure they are very different from the diaphragms ofmammals.

The ventral surface of each lung is closely covered by a thin fibrous membrane, the pulmonary diaphragm or pulmonary aponeurosis. It separates the air-sacs from the lungs. It has inserted into it a number of bands of muscle, which arise in

the vertebral ribs and are supplied by the intercostal nerves. Being connected to the pleura, the pulmonary diaphragm assists in expansion of the lungs during inspiration by the aid of these pulmonary muscles.

When the body cavity is opened from the ventral side, the viscera of the thorax and abdomen are seen to occupy the medial plane. A tightly stretched sheet of fibrous tissue on each side, the oblique septum, holds them in place and separates them from the air-sacs. The oblique septum has nothing to do with respiration (Müller, 1907). The walls of these diaphragms closely resemble the air-sacs but are of heavier texture and less transparent (Ross, 1898).

Mechanics of respiration

The open communication between the cavities of the lungs and air-sacs makes diaphragmatic breathing as it occurs in mammals impossible (Müller, 1907).

Birds have a sternum and sternal ribs and vertebrae and vertebral ribs completing the circuit of the chest (Sibson, 1846). The lungs are attached to the ribs and vertebrae so any motion of those parts necessitates a change in shape and size of lungs (Kingsley, 1912).

"The muscular mechanism by which a resting bird causes air to enter the lungs, involves elevation and depression of the breastbone through the activity of the intercostal muscles. It is necessary, however, for the breastbone to remain firm during

flight to insure anchorage of the powerful flying muscles, while the intercostal respiratory muscles are held in tension and are for the time being, not pumping fresh air into the lungs. Therefore, an internal reservoir of air is indispensible, while the flying muscles which ventilate the lungs by acting upon the air-sacs as bellows, also control respiratory movements during flight. The more rapid the flight, the greater the automatic supply of air drawn through the lungs to and from the air-sacs. Violent action in mammals interferes with respiration but in birds it increases it. That is why fast-flying birds do not 'get out of breath' or probably suffer from mountain sickness in the air of high altitudes, because the necessarily increased wing strokes bring in a compensatory supply of rarified air." (Walter, 1928).

Headley, (1893) has investigated the mechanics of respiration in birds which lead him to the following conclusions.

1. That the muscle movements necessary to flight bring about, to a great extent, the enlargement and contraction of the thoracic cavity.

2. "The latissimus dorsi which arises from the vertebrae and after passing over the scapula, is inserted in the humerus raises the backbone during the downstroke of the wing, bringing the bird's body into the position which is required for horizontal flight. Not only is the backbone raised and brought to, or nearly to, the horizontal but at the same time the ribs are straightened at the junction of their costal and sternal por-

tions, and this causes an expansion of the air-sacs."

3. The muscles which pass downwards to the ribs from the posterior ends of the scapulae help to expand the air-sacs. They also broaden the dorsal part of the thorax. The action of these muscles is assisted by the action of the scapulae.

4. Due to the great strength of the pectoral muscles, the contraction of the latissimus dorsi causes movement of the body but not of the wings. All possible work is put on the pectoral muscles so that the center of gravity may be low down.

5. Although the flight muscles help largely in respiration, much work is done by the respiratory muscles.

a. The levatores costarum arise from the vertebrae, pass backward and are attached to the ribs further back. They broaden the thorax by helping to straighten the ribs.

b. The triangularis sterni which arises from the inside of the sternum from its anterior lateral end and attaches to the sternal ribs, also broadens the thoracic cavity.

c. The external intercostals pass obliquely backward and downward between two ribs. When they contract they lower the anterior rib and raise the posterior (Fig. 67). They do not, as in man, raise the sternum because it is rendered almost immovable by the weight of the pectoral muscles, the weight of the body hanging upon the wings during flight, and the pressure of the wings inward upon the coracoid bones and the clavicals.

d. The action of the internal intercostals is so weak that they cannot be of importance in respiration.

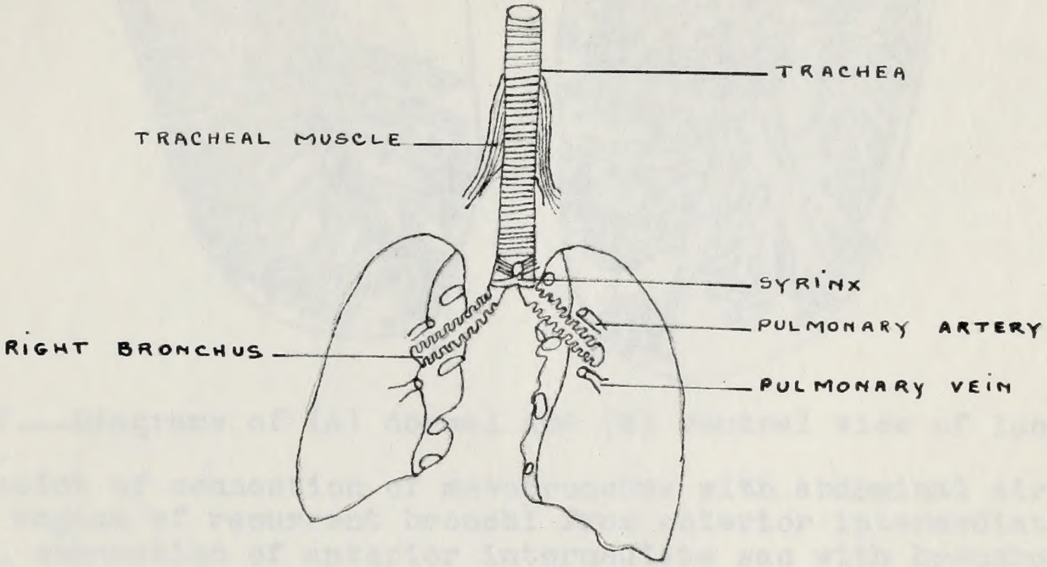


Fig. 55.—Lungs and trachea of Gallus domesticus, common chick. (From Adams.)

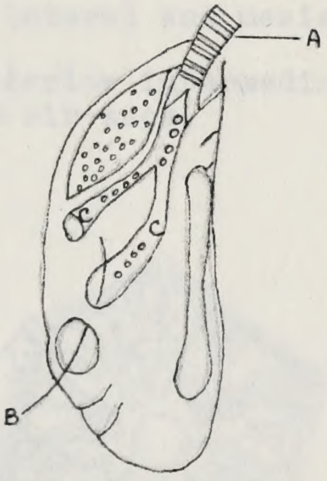


Fig. 56.—Right lung of goose, ventral view. A, bronchus; B, extremities of bronchial tubes; C, orifices of air-cells of lungs. (From Owen.)

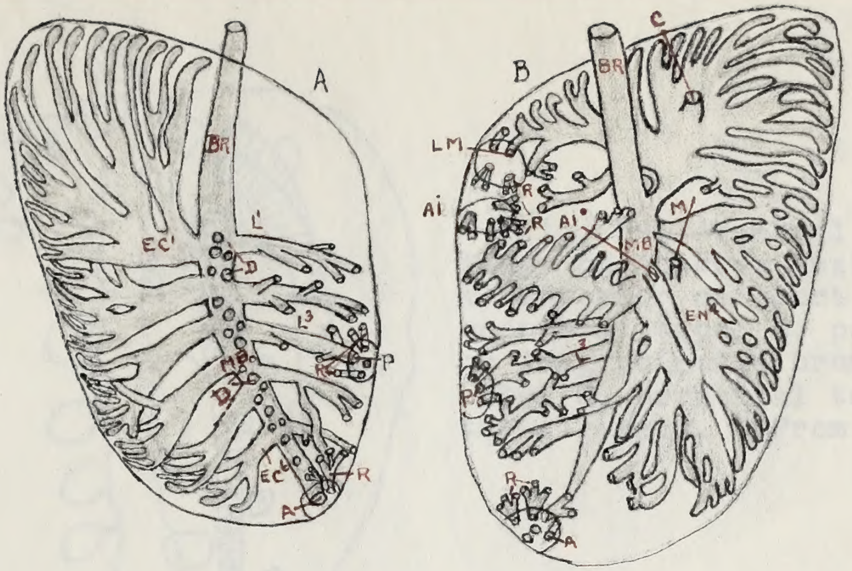


Fig. 57.—Diagrams of (A) dorsal and (B) ventral view of lung of hen.
   A, point of connection of mesobronchus with abdominal air-sac.
   AI, region of recurrent bronchi from anterior intermediate sac.
   AI , connection of anterior intermediate sac with bronchus.
   BR, bronchus.
   C, attachment of cervical sac.
   D, roots of dorsibronchi.
   EC, ectobronchi.
   EN, entobronchi.
   L, laterobronchi.
   LM, M, connection of lateral and mesial moieties of interclavicular sac.
   P, connection of posterior intermediate sac.
   R, retrobronchi from air-sacs.
   MB, mesobronchus.
(From Kingsley.)

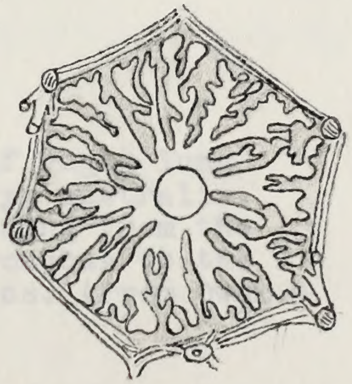


Fig. 58.—Section of lung pipe with radiating infundibula. (From Kingsley.)

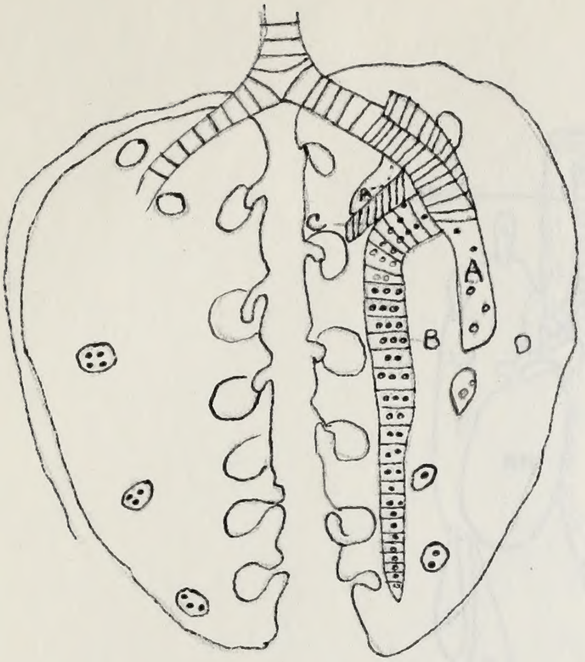


Fig. 59.—Ventral view of lungs of Apteryx australis. A, anterior or short pulmonic bronchial tube; B, posterior or long pulmonic bronchial tube; C, bronchial tube of the air-sacs. (From Owen.)

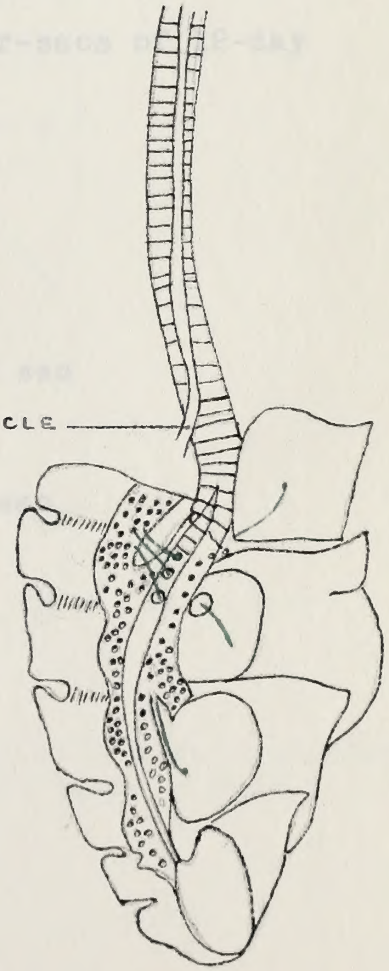


Fig. 60.—Section of right lung and air-sacs of Apteryx australis. Bristles are seen passing from the external branch of bronchus to the three anterior air-sacs. (From Owen.)

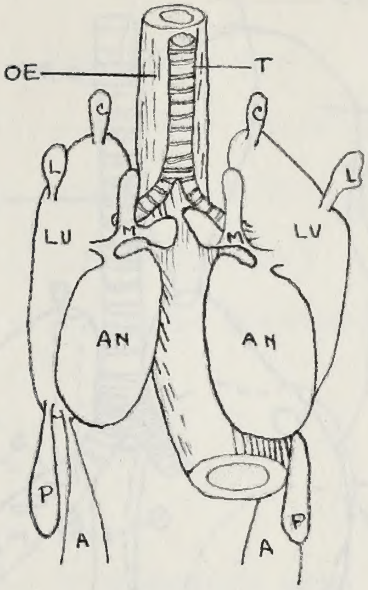


Fig. 61.—Ventral view of lungs and air-sacs of 12-day chick embryo.

AN,	anterior intermediate sac
A,	abdominal sac
C,	cervical sac
L,	lateral moiety of interclavicular sac
LU,	lung
M,	mesial moiety of interclavicular sac
OE,	oesophagus
P,	posteriorsac
T,	trachea

(From Kingsley.)

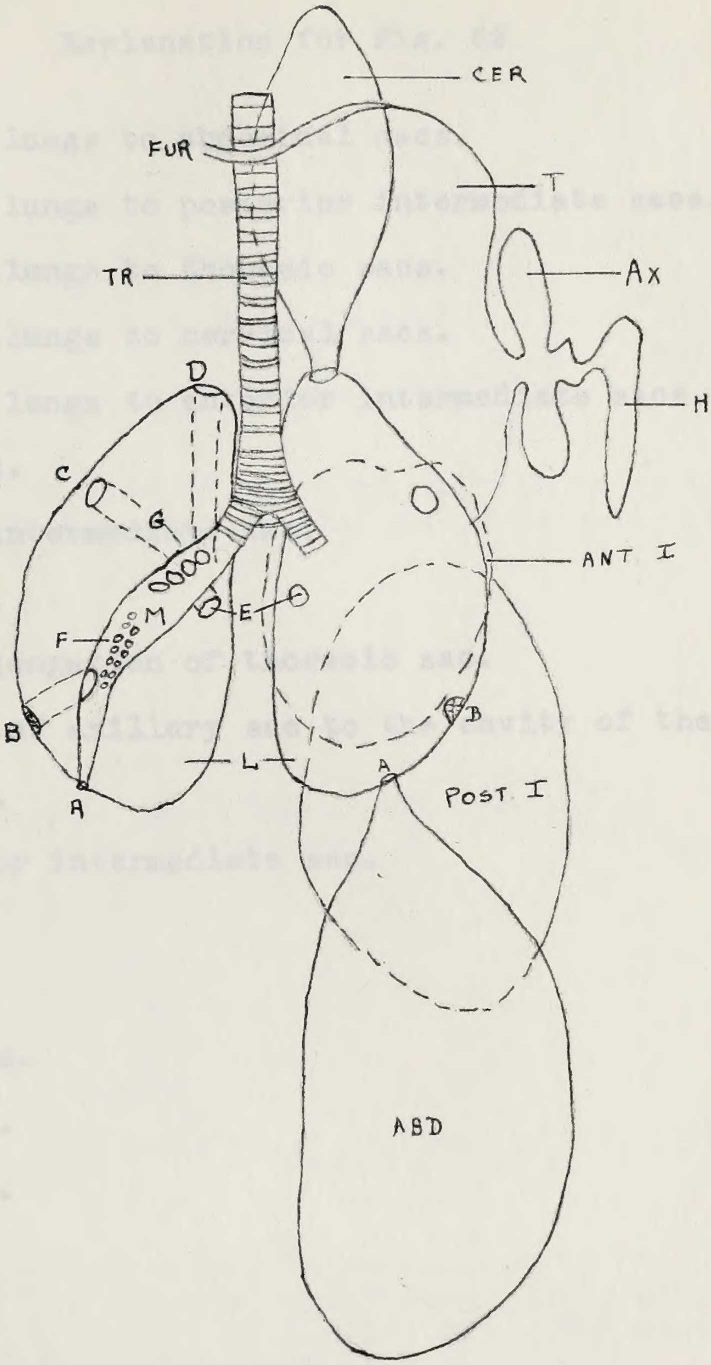


Fig. 62.—Diagram to illustrate the relative size, relation, and connection of the lungs and air-sacs in birds. Purely diagrammatic. (From Ross.)
Explanation on the following page.

Explanation for Fig. 62

A, orifice from lungs to abdominal sacs.

B, orifice from lungs to posterior intermediate sacs.

C, orifice from lungs to thoracic sacs.

D, orifice from lungs to cervical sacs.

E, orifice from lungs to anterior intermediate sacs.

ABD, abdominal sac.

ANT I, anterior intermediate sac.

T, thoracic sac.

AX, axillary prolongation of thoracic sac.

H, prolongation of axillary sac to the cavity of the humerus.

CER, cervical sac.

POST. I, posterior intermediate sac.

L, lungs.

TR, trachea.

M, mesobronchium.

F, ectobronchia.

G, entobronchia.

FUR, furcula.

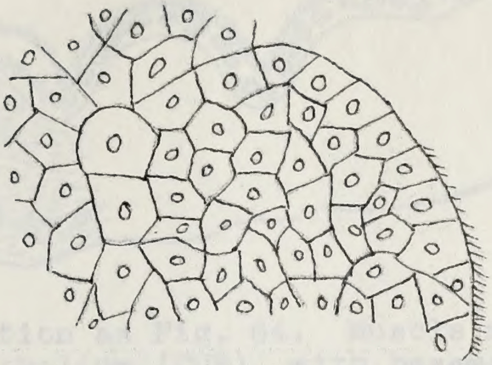
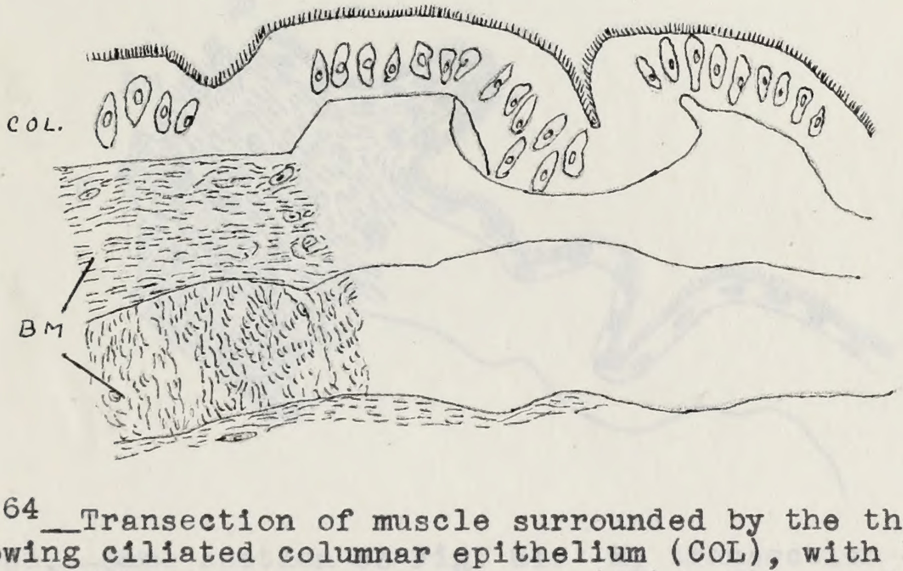


Fig. 63.—Surface view of pavement epithelium of the air-sacs, showing cilia and round nuclei in pentangular granular cells. (From Ross.)



Fig· 64__Transection of muscle surrounded by the thoracic sac, showing ciliated columnar epithelium (COL), with basement membrane of fibrous connective tissue (BM). The muscle is not drawn in this figure. (From Ross.)

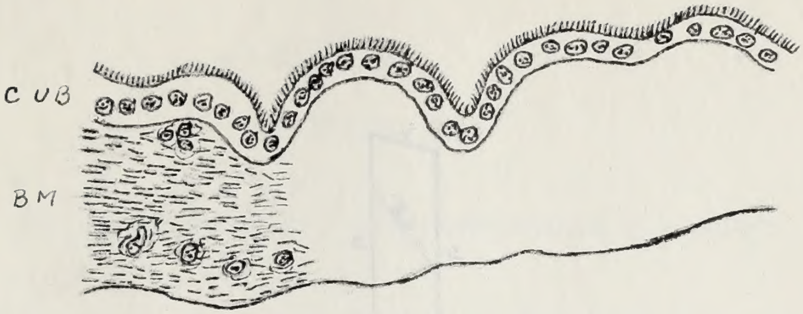


Fig. 65.—Same section as Fig. 64. Muscle not drawn. Ciliated cuboidal epithelium (CUB), with basement membrane (BM). (From Ross.)

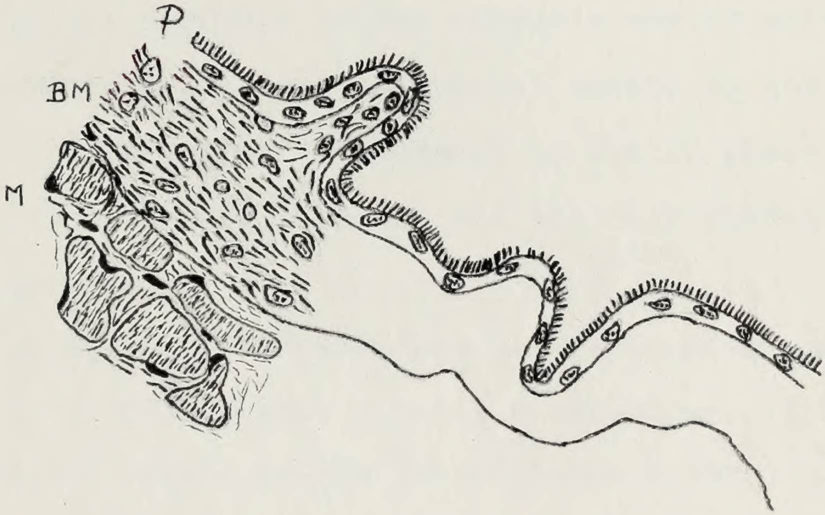


Fig. 66.—Same section as Fig. 64. M, transection of striated muscle; BM, basement membrane; P, pavement epithelium.(From Ross)

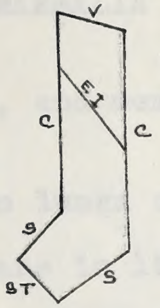


Fig. 67.—Diagram to illustrate the working of the external intercostal muscles in birds. The contraction of the muscle will lower the anterior and raise the posterior rib. C, costal rib; EI, external intercostal muscle; S, sternal rib; ST, sternum; V, vertebral column. (From Headley.)

MAMMALIA

Shape, location, and membranes of lungs

In shape, the mammalian lungs conform to the shape of the thoracic cavity and the organs in it. The outer surface of each lung which is in contact with the sides of the thoracic wall is convex. The base is concave because it rests on the convex upper surface of the diaphragm. The medium surface is concave where the lung fits around the heart.

The lungs are confined to the thoracic cavity which is completely separated from the peritoneal cavity by the diaphragm which is transverse in position except in whales where it is oblique (Kingsley, 1912). Mammals are the only animals that have a true diaphragm.

A pleural membrane derived from the peritoneum encloses the lungs. It is a double membrane forming a closed sac (Figs. 68 & 69). The inner layer, called the visceral pleura, covers the lungs. The outer layer, called the parietal pleura, lines the thoracic or pleural wall. The space between the two layers is called the pleural space, and is filled with a serous fluid that prevents friction. Toward the mid-line the pleurae form a septum between the right and left halves of the thoracic cavity. This septum is called the mediastinum.

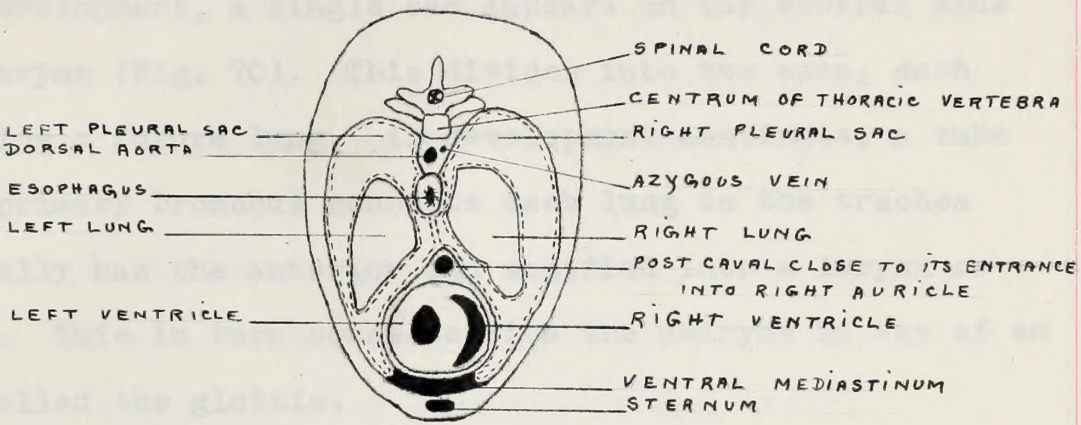


Fig. 68.—Diagram of transverse section of the thorax of the wood rabbit, Lepus cuniculus, drawn in the region of the ventricles to show the relation of pleurae, mediastinum, etc. Ventral view. The lungs are contracted. (From Parker & Haswell.)

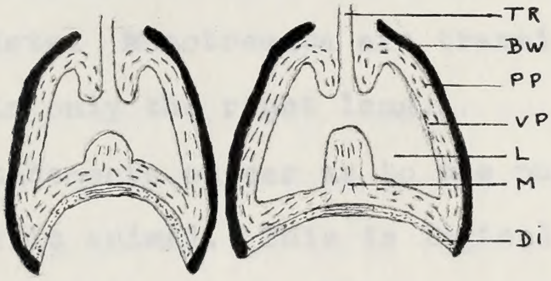


Fig. 69.—Human lungs in thoracic cavity. A, air expired by raised diaphragm and contracted ribs; B, air inspired by lowered diaphragm and relaxed ribs; BW, body wall; DI, diaphragm; L, lung; M, mediastinum; PP, parietal pleura; VP, visceral pleura. (From Walter.)

Development

In development, a single sac appears on the ventral side of the pharynx (Fig. 70). This divides into two sacs, each representing a future lung. As development continues, a tube called a primary bronchus connects each lung to the trachea which usually has the anterior end modified into a larynx or voice box. This in turn connects with the pharynx by way of an opening called the glottis.

Division into lobes

Usually the lungs are divided into lobes. When asymmetry occurs, and it usually does, there are more lobes on the right than on the left side.

The following groups (Walter, 1928) show no division into lobes: Cetacea, Sirenia, Proboscidea, Hyracoidea, and most Perissodactyl Ungulata. Monotremata are transitional because lobes are present in only the right lung.

Conflicting statements appear as to the number of lobes in the lung of a specific animal. This is logically explained by Young and Robinson (1888) who say, "It is probable that the number of lobes is liable to variation or that there is a difference of opinion as to exactly what constitutes a lobe."

Examples and illustrations of lobulation

In the Kangaroo (Parsons, 1896) the right lung is much larger than the left and has a well marked azygous lobe. The right lung has two notches on the ventral border and the left has one.

The cat (Reighard & Jennings, 1930) has four lobes in the right lung and three in the left lung (Fig. 71). In the cat, the lobes are not divided into lobules (Water, 1860).

In the spotted hyena, Hyaena crocuta, (also called Hyaena maculata) Watson & Young (1897) found six lobes in the right lung and three in the left lung (Fig. 72). In the right lung, the sixth is the azygous lobe. Hyaena crocuta differs from both the other species of hyena, where the right lung possesses four lobes and the left three. Watson (1881) in the examination of another specimen of Hyaena crocuta found five lobes on the right and three on the left.

More variation is noted in the striped hyena, Hyaena striata. The specimen examined by Young & Robinson (1888) showed three lobes on the right and one on the left. These authors quote Meckel as finding four lobes on the right and three on the left, and Daubenton four on the right and two on the left.

In Proteles (Flower, 1869) the lungs are deeply divided into distinct lobes, four on the right, three on the left. On the right, the fourth lobe is the azygous lobe.

In the ferret-badger, Helictis personata, (Beddard, 1905) the lungs consist of four lobes on the right, and two on the left.

The white rat (Adams, 1933) shows four lobes on the right and one on the left (Fig. 73). Martin & Moele (1884) give for the common brown rat, three on the right and two on the left.

James Murie (1874) describes the lungs of the sea lion (hair seal), Otario jubata. When inflated they are usually long in shape. The right lung has four lobes, the fourth being the azygous lobe. The left has three main lobes.

He also describes the lungs of the walrus, Trichechus rosmarus, Linn (Fig. 74). They, too, are very elongate, with notched anterior margins.

In man (Walter, 1928) there are three lobes in the right lung and two in the left (Fig. 75). The uppermost odd lobe on the right lies behind the right pulmonary artery while the absence of a corresponding lobe on the left side allows room for the large aortic arch.

The bronchial tree

The bronchial tree in the majority of mammals is asymmetrical. Huntington (1920) says "... pulmonary asymmetry is encountered in at least 95% of the mammalian genera and species whose bronchial trees are recorded."

The bronchi are called eparterial if they lie above the pulmonary artery and hyparterial if they lie below it (Fig.76).

The pulmonary artery crosses the main bronchus formed by the bifurcation of the trachea, and this point divides the lateral bronchi into eparterial and hyparterial.

The hyparterial bronchi are always well developed and consist of a double row of lateral bronchi. The eparterial, though, may consist of a single external lateral bronchus on either side. Usually the left one disappears, leaving only the right, which also may disappear. Usually, the eparterial bronchus occurs on the right side. The known exceptions (Goodrich,1930) are the genera in which it occurs on both sides (Bradypus,Phoca, Equus, Auchenia, Elephas, Phocaena, Delphinus, Cebus) and Hystrix and Taxidea in which it does not occur at all. The latter possess lungs of very abnormal structure.

The eparterial, whether developed on one or both sides, may arise from the trachea instead of from the main bronchus (Wiedersheim, 1897). In the Artiodactyle Ungulates and the Cetacea, it may arise from the trachea. In Auchenia and Delphinus, its origin is bronchial on the left and tracheal on the right (Goodrich, 1930).

The blood vessels show the relationship between the lobes of the lungs. Since the anterior lobe of the right lung belongs to the eparterial bronchus, it is the right middle lobe that corresponds to the anterior lobe on the left side, in man.

Types of branching in the bronchial tree

The two most common types of branching are the monopodial, in which lateral branches are given off from a main axis that extends through the structure, and dichotomous, in which the main axis divides repeatedly into two branches. A few statements from Miller (1913) show the variations in conclusions about the type of branching. From the study of the cat, he concluded that the main series of branches were monopodial. He lists other opinions on the cat and other animals as follows: Aeby (on the cat) monopodial; Ewart, and Huntington (on the cat) dichotomous but uneven dichotomy; Müller (on the whale) monopodial; His (on man) a mixed type, the first divisions being monopodial but producing new bronchi by dichotomous division.

Epithelium in the alveolar wall

Although the presence of epithelium in the alveolar wall was once a much debated subject, most authorities now agree it is present.

Shea (1936) gives evidence in favor of the existence of epithelium as a result of his studies of the alveolar wall of the rat, guinea pig, and rabbit. He claims "positive evidence in favor of the view that

(1) flattened epithelial cells... exist in considerable numbers in the lung;

(2) these flattened cells possess very thin membranous peripheral parts which extend widely from the relatively thickened nuclear portion and cover the neighboring capillaries;

(3) that it is these cells with their thin expansions that collectively constitute the 'alveolar membrane' which is therefore a cellular membrane...;

(4) that these cells show the probability of a continuous epithelial lining of the lung alveolus;

(5) that as Snow-Miller has already pointed out, these cells can and do separate off from the epithelial sheet and form the rounded epithelial cells described by many workers."

The presence of epithelium in man is stated by Waters (1860); Dwight (1919); Goodrich (1930); Miller (1937).

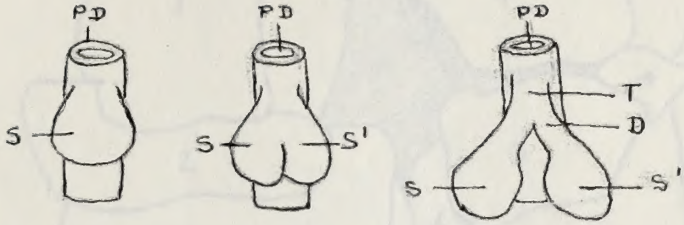


Fig. 70.—Showing mode of development of mammalian lungs. PD, primitive alimentary tube; S,S', lung-sacs, at first unpaired; T, trachea; B, bronchus. (From Wiedersheim.)

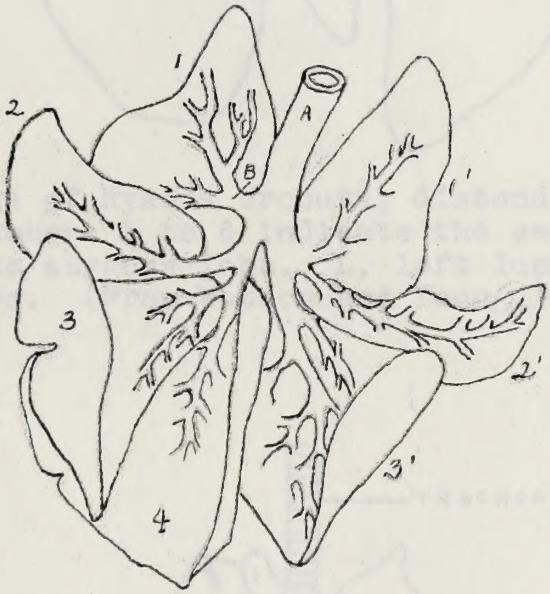


Fig. 71.—Ramifications of the bronchi, with outlines of the lobes of the lungs of the cat, ventral view. A, trachea; B, eparterial bronchus; 1 to 4, lobes of right lung; 1' to 3', lobes of left lung. (From Reighard and Jennings.)

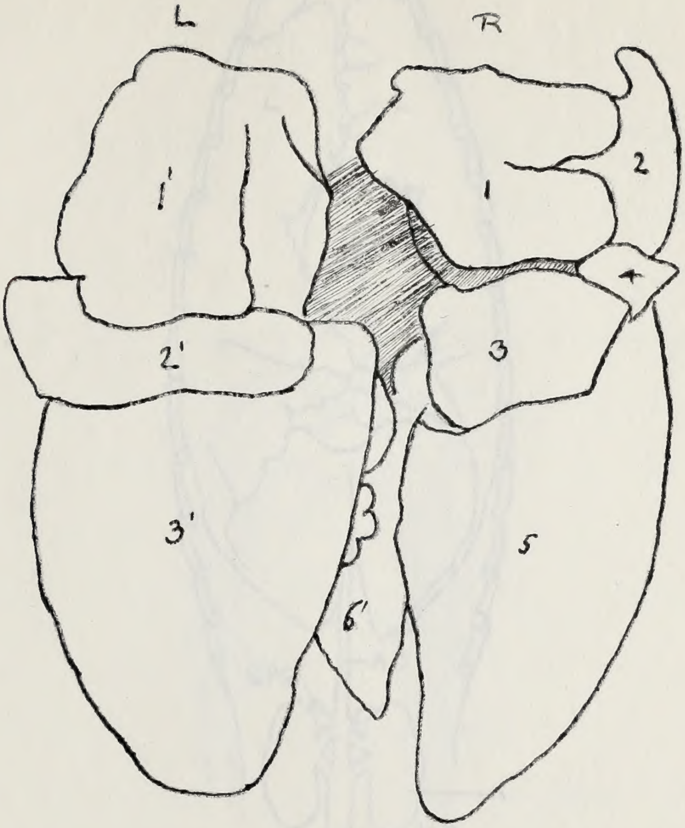


Fig. 72.—Lungs of Hyaena crocuta, distended. Dorsal view. R, right lung. Numbers 1 to 6 indicate the separate lobes, number 6 being the azygous lobe. L, left lung. Numbers 1' to 3' indicate its lobes. (From Watson and Young.)

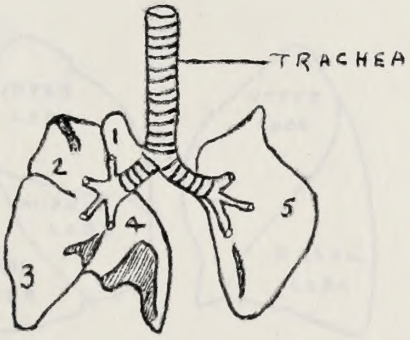


Fig. 73.—Lungs and trachea of white rat. (From Adams.)

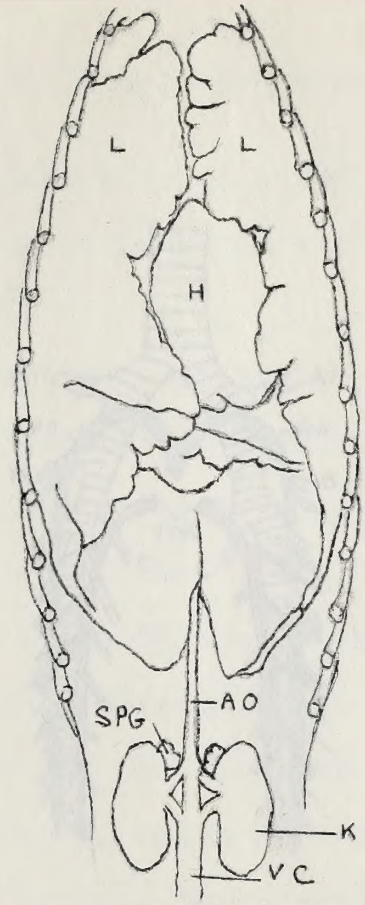
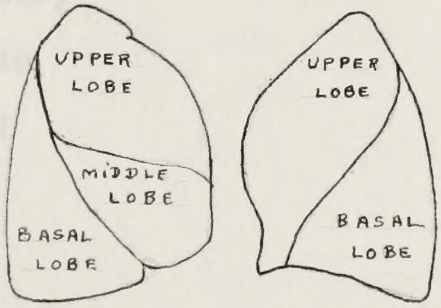


Fig. 74.—Dissected view of the thoracic and renal organs of the walrus, Trichechus rosmarus, Linn. The sternal wall with cartilages, diaphragm, liver, stomach, and intestines have been removed. L, lungs; H, heart; AO, abdominal aorta; K, kidney; SPG, right suprarenal gland; VC, vena cava. (From J. Murie.)



Right Left

Fig. 75.—Lobes of human lung. (From Walter.)

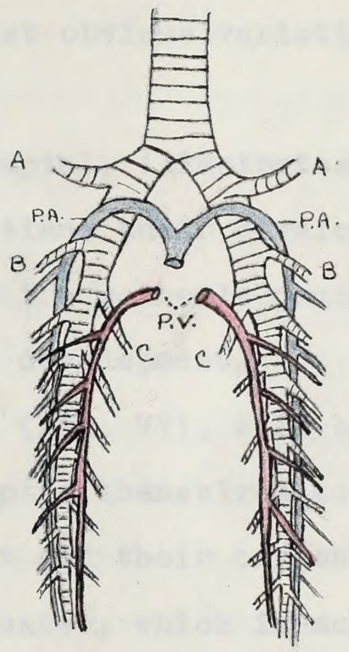


Fig. 76.—Arrangement of bronchi in mammals, ventral view.

A,A, eparterial bronchus

B,B, series of ventral hyparterial bronchi

C,C, series of dorsal hyparterial bronchi

P.A. pulmonary artery

P.V. pulmonary vein

(From Wiedersheim.)

RESPIRATION IN SPECIFIC MAMMALS

The study of representatives of three different groups of animals will show the most obvious variations in lung structure in mammals.

The opossum, a marsupial, illustrates the unusual case where immature young continue their development after birth. During the time spent in the mother's pouch, the lungs, as well as other organs complete development.

Sirenia and Cetacea (Fig. 77), will be discussed as examples of mammals that have adapted themselves to life in and under water, although they must get their oxygen from the air. This ability to remain under water, which in most warm blooded animals is very limited "appears in several orders of birds; among mammals, besides the aquatic manatees, whales, and seals, there are for example, muskrat, beaver, hippopotamus, and otter" (Irving, 1934).

Man is used as the example of the most typical mammal that both lives and breathes on land.

OPOSSUM*

New born opossums are about 10 mm. long. At birth their lungs are composed of a few large air chambers that open almost directly into the main bronchus. Air-sacs and alveoli are lacking. Respiration has to be carried on in these modified bronchi and bronchioles while the infundibular portions of the lungs are developing. Therefore these large air chambers are lined with special epithelium for respiration. As development progresses they give off branches and enlarge the bronchial tree. There are bands of muscle fibers running circularly around the main bronchus. They may help to contract the lung and force the air out during expiration. By the time the opossum has reached 14 cm. in length the air-sacs have developed, and from them the alveoli are given off.

*From Bremer (1904)

SIRENIA

Sirenia are large aquatic mammals, popularly called sea-cows. There are two genera; Manatus, found in the Atlantic and in a small section on the east coast of Africa; and Halicore (dugong), found in the South Pacific and Indian Oceans. They inhabit shallow water, often near the mouths of rivers, which they ascend.

Parker (1922) studied the breathing habits of the Florida manatee, Trichechus latirostris (Harlan), in the Miami Aquarium. The animal remained submerged for hours at a time, except to come to the surface to breathe. Two or three respiratory acts occured, twenty seconds to three minutes apart. The longest time any specimen remained under water was sixteen minutes.

Microscopic study of manatee lungs*

Terminal bronchioles have a diameter of .6 to .3 mm. at the point where they enter the air-sacs. This is large compared to other mammalian bronchioles. They are lined by cuboidal or columnar epithelium, which ends at the union of the terminal bronchiole and its air-sac. This indicates a boundary line between the conducting tubes and the respiratory area. In this case the respiratory area does not extend into the air-tubes.

The cartilage is highly developed and extends into the walls of the smallest bronchioles and their openings into the air-sacs.

*From Wislocki (1935)

Smooth muscle and elastic tissue are found in the bronchioles, but there are no myo-elastic sphincters in the terminal bronchioles as in the porpoise. The elastic tissue is mostly in the form of a thin layer of fibers lying between the cartilages and the lumen of the bronchiole.

The air-sacs are very large, especially in the periphery under the dorsal pleura. These sacs are cylindrical in shape. Their lengths may reach 6 mm. and their diameters 1 to 2 mm. On the ventral surface of the lung, the air-sacs are never elongated. In the interior of the lung, they are smaller and polygonal in shape.

The septa bounding the air-sacs are composed of much collagenous material, some smooth muscle, and a small amount of elastic tissue. The air-sacs are subdivided by septal folds, along whose margins the muscle and elastic tissue intermingles, forming dense myo-elastic bundles, which probably help to control the size of the sacs.

The capillaries which form a double bed in the walls of the alveoli are separated from each other by collagenous tissue which lies in the center of the septum.

Wislocki could not with certainty distinguish the presence of an epithelial lining in the alveoli, but in some cases observed a distinct layer of cells on the surface of the alveolar wall. This he believes was epithelium.

The pleura is very thick, varying from 0.3 to 0.5 mm., which is much thicker than in terrestrial animals. It is well

vascularized. Beginning with the outside, it is composed of the following layers; a layer of mesothelial cells; a layer of collagenous tissue; a thick layer of elastic tissue; a vascular layer consisting of blood vessels imbedded in a layer of white fibers and smooth muscle bundles; and innermost a layer of delicate fibro-elastic tissue containing capillaries.

CETACEA

Because most Cetacea live in the open ocean, often in water of great depths, a study of their habits and anatomy is rendered difficult. Wislocki (1929) studied the porpoise, Tursiops truncatus; Wislocki and Belanger (1940) studied a group of whales including the Blue Whale (Balaenoptera sibaldii), the Finback (Balaenoptera physalus), and Sperm Whale (Physeter megalocephalus). The lungs of all three were similar. The whales studied by Haynes and Laurie (1937) were the Finback (Balaenoptera physalus), Humpback (Megaptera nodosa), Sperm Whale (Physeter catadon), and the Southern Right Whale (Balaena australis).

The Blue Whale studied by Laurie (1933), and Wislocki and Belanger (1940) is so-called because it has a bluish caste. It is the largest mammal that ever lived, either on land or sea The specimen examined by Laurie (1933) weighed 63 tons but some reach a length of 100 feet and weigh as much as 115 tons. They would equal in length and surpass in weight the extinct dinosaurs (Kellogg, 1940). The lungs of a Blue Whale weigh over a ton, so anatomical study is confined to sections (Haynes and Laurie (1937). When cut, the collapsed lung resembles a rubber sponge permeated with blood (Haynes and Laurie, 1937).

Adaptations for breathing in water

Cetacea are adapted for life in the water in many ways, but perhaps the "blowhole" is the most important in breathing.

These external nasal openings are located on the top of the head. Whalebone whales have two, but in all other Cetacea the two are united into one. Since the blowholes are located on top of the head, the animals can breathe without exposing much of the body above the surface.

The forward part of the larynx extends as a very long appendage into the cavity of the blowhole (Racovitza, 1903). The tube to the blowholes is usually almost straight, except in the Sperm Whale where it runs obliquely forward (Miller and Gidley, 1938). This makes a continuous connection between the blowhole and the lungs. Cetacea swallow their food under water. The food passes into the esophagus on each side of the closed-off larynx (Racovitza, 1903), and the water cannot go into the lungs by way of the mouth. When the animal is under water, the blowhole is kept closed by an elaborate set of pocket valves (Norman and Fraser, 1938).

Before expiration takes place, the blowhole is protruded rapidly and spouting does not occur until the blowhole is out of the water. The orifice of the blowhole is small and air is expelled in a narrow column with force. During inspiration the orifice is wide open and air is taken in suddenly.

Additional adaptations are seen "in the whole topography of the chest, ribs, diaphragm, and neck, as well as in the structure of the trachea and lungs themselves" (Wislocki, 1929). The chest is barrel shaped and the diaphragm oblique, thus allowing greater extension of the lungs. The neck is relatively

immobile and the trachea is short. The structural rigidity due to the extensive cartilage resists the outside pressure.

Another adaptation is given by Beddard (1900) regarding the blood vessels. In many parts of the whale's body the blood vessels form networks or "retia mirabilia" produced by the breaking up of an artery into minute arterioles. The result is that the flow of blood is slowed up at this point and the oxygen more fully utilized by the surrounding tissues. These networks of blood vessels are located near organs that need abundant oxygen.

Inspiration and expiration in the whale[*]

After a period of submergence the whale comes to the surface and at once makes a prolonged and forceful expiration called a "spout" or "blow". The warm moist air given off condenses if the atmosphere is cold enough. If the air is calm and the animal is moving slowly, the spout is vertical, but if there is a wind or the animal is moving rapidly the spout is inclined.

The duration of the spout varies, the larger Cetacea spouting longer than the smaller ones. Racovitza (1903) gives the following examples; 5 to 6 seconds for the sulphurbottom whale; 3 or 4 seconds for the humpback; and 2 seconds for the porpoise. The noise of the spout varies in intensity with the size of the animal, being scarcely audible in the common dolphin and very loud in the sulphurbottom, which also holds the highest spout record, 49 feet.

[*] From Racovitza (1903)

Following the spouting, the whale makes a series of shallow dives, each of which is followed by an expiration and inspiration. The spouting which follows these dives is not so high. The whales that dive the deepest or stay under water longest take the greatest number of ordinary inspirations before prolonged submergence. The Sperm Whale has a record of 60 to 70 shallow dives. It has remained under water an hour and ten to twenty minutes. In this whale, long submergence is important because it feeds chiefly on cuttlefish which live at great depths.

Following the series of shallow dives there is a long deep inspiration after which the whale plunges to the depths for a quarter of an hour or more.

Lung structure in cetacea

Cartilage

In the bronchial tree of the Cetacea, there is a complex cartilaginous development which allows a high degree of compressibility caused by the increased outside pressure.

In the porpoise, the cartilages of the trachea and bronchi are circular and closed. There is no membranous part. The rings are not completely separate, but fuse with each other at irregular intervals, producing a lattice work. In the bronchioles bearing sphincters, the cartilaginous bands tend to alternate in position with the sphincters. The cartilage extends down to the last sphincter that opens into the air-sac. (Wislocki, 1929).

In the whale, the extent and arrangement of the cartilage is the same as in the porpoise (Wislocki & Belanger, 1940).

Respiratory division of bronchial tree

In the porpoise, the first muscular sphincter marks the point where the conducting division of the bronchial tree ends and the respiratory division begins. The first sphincter is followed at short intervals by a series of similar sphincters 6 to 18 according to the length of the bronchiole. These sphincters occur up to the point where the bronchioles, now 0.2 mm. in diameter, enter the air-sacs. In other words, the last sphincter marks the entrance to the air-sacs. (Wislocki, 1929).

Beginning with the first sphincter the epithelium changes from the high columnar type of the conducting bronchioles to a flattened respiratory type in the respiratory bronchioles. This extension of the respiratory surface into the bronchioles increases the respiratory area more than in other mammals where the bronchioles bear only scattered alveoli on their walls. (Wislocki, 1929).

In whales, there are no traces of muscular sphincters in the terminal bronchioles (Wislocki and Belanger, 1940).

Air-sacs

In the porpoise, when the air-sacs are distended, they appear polygonal, oval, or elongate in shape. The air-cells

or alveoli are separated by strong septa which contain elastic tissue on each side of which is a network of capillaries. No muscle tissue was found by Wislocki (1929) in the walls of either the air-sacs or the alveoli, although there were delicate bundles of myo-elastic fibers in the walls of the air-sacs.

In the whale, the air-sacs are enormous. Some examples from Wislocki and Belanger (1940) follow:

	Diameter of air-sacs	of alveoli
Blue Whale	4.71 mm.	0.40 mm.
Finback	2.00 mm.	0.45 mm.
White Whale	.90 mm.	0.35 mm.

The walls of the air-sacs and inter-alveolar septa are excessively thick.

	Diameter of walls of air-sacs.	Diameter of walls between alveoli.
Blue Whale	240 u	60 u
Finback	60 u	20 u
White Whale	30 u	20 u
Porpoise (Tursiops)	75 u	20 u

The larger septa that project into the portion of the air-sac adjacent to the bronchiole have thick bundles of muscle and elastic tissue forming myo-elastic bundles. These run in a direction circular to the long axis of the air-sacs. (Wislocki and Belanger, 1940).

Laurie (1933) describes a "heavy elastic bundle circumscribing each infundibulum." Wislocki and Belanger say these bundles are not purely elastic tissue, but are the myo-elastic sphincters mentioned above in the larger septa.

Myo-elastic bundles are present to some degree in all Cetacea, but myo-elastic sphincters are a special structure found only in the small species (Wislocki, 1929).

The elastic tissue predominates in the bundles, whereas the muscle tissue predominates in the sphincters. Myo-elastic bundles are homologous to the delicate strands of muscle described in the alveolar ducts of many other mammals. (Wislocki and Belanger, 1940).

The function of the myo-elastic sphincters in the porpoise is to close off the air-sacs and respiratory bronchioles after inspiration and imprison the air in them, thus preventing a gradual collapse caused by the increased pressure from the outside while the animal is submerged. The air is thus kept in contact with the respiratory surface. The sphincters also act as antagonists to the action of the elastic tissue. (Wislocki, 1929).

In one porpoise, the small harbor porpoise (Phocaena communis) no special myo-elastic closing of the air-sacs or bronchioles is found. This porpoise is not able to remain submerged so long or to go to such great depths as the others. The one known whale in which myo-elastic sphincters are found is the small white whale. (Wislocki and Belanger, 1940).

The myo-elastic bundles serve the same purpose as the sphincters. They close off the respiratory portion of the lung. The elastic fibers help rapid expulsion of air during expiration. (Wislocki and Belanger, 1940).

The elastic tissue in the air-sacs helps the lungs to collapse quickly and completely when the whale expires, so that the only air left in the lungs is that in the "dead-space" or non-flexible portions of the lungs such as the air-tubes. The degree of collapse in a whale's lung is great due to the large quantity of elastic tissue in both the lung substance and the pleura. (Haynes and Laurie, 1937).

Lack of epithelium

In the whale, the interalveolar septa are bounded on both sides by an extensive capillary network on which no epithelial lining can be identified (Wislocki and Belanger, 1940). The blood is separated from the air-spaces by the thin capillary endothelium (Haynes and Laurie, 1937). "The lack of alveolar epithelium and exposure of the capillary network to the respiratory gases is believed to be unknown hitherto in lungs of land mammals which have been examined. In the latter epithelium is always present." (Haynes and Laurie, 1937).

Pleura

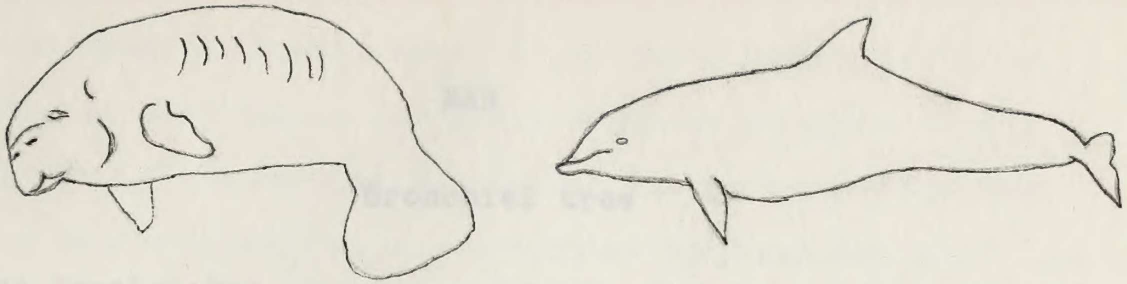
In the porpoise, the pleura varies from 0.5 to 1 mm. in thickness. It is composed of dense fibro-elastic tissue, well

vascularized. No smooth muscle is present. (Wislocki, 1929).

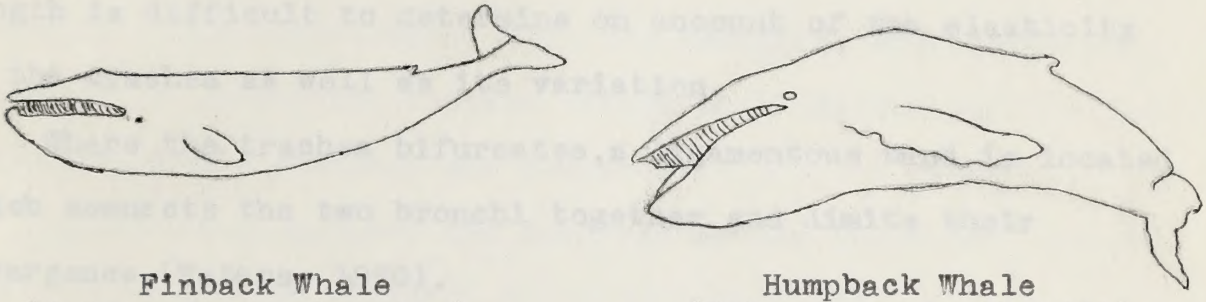
In the whale, the thickness of the pleura differs in different species, but the average thickness is 5 mm. Elastic tissue is very abundant. (Haynes and Laurie, 1937).

Diaphragm

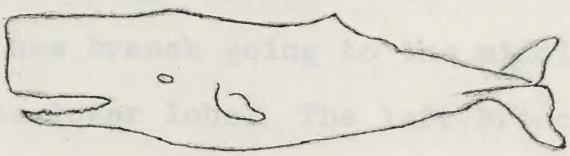
The diaphragm in whales is oblique in direction (Beddard, 1900). It is connected ventrally to the abdominal muscles and passes dorsally in an oblique line to the posterior end of the vertebral column (Beale, 1839). The oblique diaphragm allows for a larger thoracic cavity in which the lungs extend further back as well as further forward than in quadrupeds (Wislocki, 1927). This increased length of lungs takes the place of lobulation which is lacking.



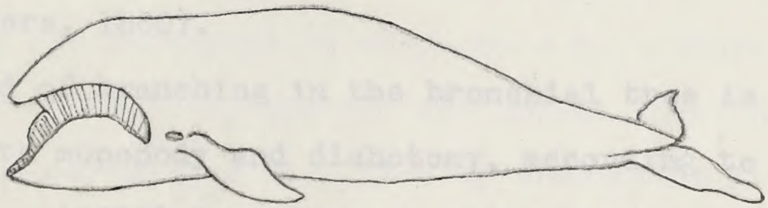
Manatus Porpoise (Tursiops truncatus)



Finback Whale (Balaenoptera physalus) Humpback Whale (Balaenoptera sibaldii)



Sperm Whale (Physeter catodon)



Southern Right Whale (Balaena australis)

Fig.77.—Animals adapted to living in water but breathing air.

MAN

Bronchial tree

The trachea has an average length of 4 to 4 3/4 inches in man, and 3 2/3 to 4 1/2 inches in woman (Dwight, 1919). The length is difficult to determine on account of the elasticity of the trachea as well as its variation.

Where the trachea bifurcates,a ligamentous band is located which connects the two bronchi together and limits their divergence (Waters, 1860).

The right bronchus has three branches, one for each lobe of the lung. It first divides into two unequal branches, the smaller of which goes to the upper lobe. The other branch divides again, the new branch going to the middle lobe, and the original stem to the lower lobe. The left bronchus gives off a branch to the upper lobe and then passes into the lower lobe. The primary bronchi subdivide until finally they end at the air-sacs. (Waters, 1860).

The method of branching in the bronchial tree is a combination of both monopody and dichotomy, according to most authors. Waters (1860) describes the main bronchus as dividing usually dichotomously into primary branches; these, by dichotomous or trichotomous division form secondary branches. Tertiary and quarternary branches are formed by dichotomous division. His conclusion was that dichotomous division was the

commonest type, although there was no great regularity.

Several more recent investigators seem to agree on a combination of the two types. Ogawa (1920) states that the alveolar duct divides two to nine times to reach the air-sacs, and that in this branching both monopody and dichotomy are found. Willson (1922) says, "The method of branching of the bronchioles is dichotomous until the terminals are approached, and then the branching becomes irregular." Miller (1937) finds alternation of dichotomy and monopody.

Anastomoses between the branches of the bronchial tree do not occur (Macklin, 1929).

Structure of the trachea and larger bronchial tubes

The trachea has 16 to 19 rings of cartilage (Dwight, 1919); 16 to 20 (Miller, 1937); 16 to 21 (Waters, 1860). In the trachea and larger bronchial tubes, the cartilage is in the form of rings incomplete dorsally. The rings show marked irregularities such as splitting, or fusing with adjoining rings.

The rings are connected to each other by a dense layer of connective tissue (Miller, 1937). The dorsal space between the ends of the cartilages is filled by a membrane made up mostly of the fibers of the trachealis muscle. These fibers run transversely with only a few scattered longitudinally. During inspiration the muscle layer relaxes, thus increasing the lumen of the tubes. During expiration narrowing is caused by contraction of the muscle fibers. The X-ray and bronchioscope

show that these changes occur (Macklin, 1929). The muscular membrane is attached to the inner surface of the cartilages in man, but to the outer surface in some other animals. The bundles are frequently branched and often link together cartilages of different levels.

Throughout the bronchial system there is intermingled with the muscular layer, a loosely woven layer of elastic fibers arranged circularly, forming a myo-elastic layer (Macklin, 1929).

Situated between the muscular layer and the epithelium is a layer of closely interwoven elastic fibers which run lengthwise along the air tubes from the larynx to the alveoli (Macklin, 1929). During inspiration, the elastic layer stretches, increasing the length of the tubes. During expiration, the elastic layer relaxes, shortening the tubes.

The epithelium consists of several layers made up of the following kinds of cells: basal, just above the basement membrane; intermediate, extending from the basement membrane to the surface of the epithelium; ciliated columnar in the bronchi and ciliated cuboidal in the bronchioles, extending from the basement membrane through the entire thickness of the epithelial layer; goblet cells, also extending through the entire thickness of the epithelium (Miller, 1937).

The epithelium is extensive enough to line the tracheal wall when it is in a stretched condition. When the trachea is narrowed by contraction of the circular muscular layer the epithelium forms lengthwise ridges (Macklin, 1929).

Structure of the finer bronchial tubes

Eventually a point is reached in the smaller bronchial tubes where the cartilagenous rings are no longer present. Instead, crescent shaped cartilage plates are arranged in broken circles with no membranous space dorsally. This makes all sides of the air tubes equally resistant to pressure (Waters, 1860).

The point where cartilage begins to be lacking entirely is in bronchi between .06 and .07 mm. in diameter on an average (Miller, 1937). Before cartilages disappear altogether, fragments are found only at points where lateral branches are given off by the bronchial tubes (Waters, 1860).

When the point is reached where there is no dorsal space between the ends of the cartilagenous rings, the transverse muscle fibers gradually extend in a netlike arrangement around the entire tube instead of just between the ends of the cartilages (Macklin, 1929).

In the smaller bronchioles, especially the terminal bronchioles, the muscle tissue is relatively better developed, but from there on it becomes less dense in the respiratory bronchioles and alveolar ducts. In the latter the strands are arranged in a mesh-like form. The spaces in the mesh are occupied by openings leading to other alveolar ducts, alveolar sacs, or alveoli. (Macklin, 1929).

Elastic fibers are intermingled with the muscular layer,

which helps give an evenness to the dilation and recoil mechanism (Macklin, 1929).

When bronchioles reach a size of about 1 mm.in diameter, the epithelium diminishes in thickness. The same kinds of cells found in the trachea and bronchial tubes are present, but ciliated cells outnumber the others. Just before the appearance of alveoli, the epithelium changes still more. The ciliated cells change from columnar to cuboidal in shape. Goblet cells disappear. In respiratory bronchioles the ciliated cells gradually disappear and are replaced by non-ciliated cuboidal epithelium which exists throughout the respiratory bronchioles. In the alveolar ducts, the cuboidal cells become flattened into squamous epithelium. (Miller, 1937).

Lung unit

A unit of lung structure is the lobule which consists of a respiratory bronchiole and all the tissue branching from it (Figs. 78 and 79). Each lobule is arranged so as to give a great increase in respiratory surface. The terms applied to the various structures are numerous and are here briefly explained since they occur in the works of all authors, although there is some variation in the choice of terminology for a particular structure. Macklin (1929) makes the greatest number of subdivisions defined briefly as follows: terminal bronchioles which indicate the last portion of the purely conducting airway; respiratory bronchioles referring to the first tubes bearing

alveoli on their walls; alveolar ducts leading from respiratory bronchioles and opening into the air-sacs or infundibula; alveoli which are the individual air-cells in the walls of an air-sac. Miller (1937) uses, in addition, the term atrium to designate an expansion between the end of the terminal bronchus and the air-sac. Ogawa (1920), Willson (1922), and Macklin (1929) object to the term atrium because they find no definite area to which this additional term applies. Macklin objects also to the term infundibulum because it suggests a funnel shape, which is not the typical shape of an air-sac.

An alveolar duct divides two to nine times to reach the air-sacs (Ogawa, 1920). The alveolar ducts bear on their walls not only alveoli but sometimes, in addition, air-sacs of various sizes. Air-sacs as compared to alveoli are relatively more numerous toward the peripheral ends of the ducts, while isolated alveoli are more frequent near the proximal ends (Macklin, 1929).

The alveoli on the walls of the bronchioles are larger and more easily seen in the lungs of some of the lower mammals, than in human beings. In man, they are sometimes not present at all. They appear to diminish in number with advancing age. The more distended the lungs, the more the alveoli are obliterated. (Waters, 1860).

Structure of an air-sac

The air-sacs are arranged in groups, side by side (Fig.80), in nearly circular form, but due to pressure they become

flattened (Waters, 1860). Each air-sac is divided by septa into alveoli. The number of alveoli in one air-sac is from 5 to 20, with 11 the average (Ogawa, 1920). Waters (1860) quotes Rossignol as giving the number 10 to 20. Alveoli have an average diameter of 1/100 of an inch (Howells,1901). The estimated number of alveoli is 725,000,000 (Howells,1901).

There is no communication between the air-sacs of adjoining lobules (Waters,1860; Miller,1893). As a proof, Miller states that a fluid cannot be injected from one bronchiole into another. There is no communication between adjacent air-sacs, or through the walls of adjacent alveoli (Willson, 1922). So-called "alveolar pores" are not to be confused with communication between the alveoli (Miller,1937). They are openings in the alveolar wall but are the results of some disease process where the epithelium is shed on both sides of the alveolar septum.

The walls of the air-sacs and alveoli have essentially the same structure except that the alveolar walls are more delicate. Alveolar walls are made up of a single network of capillaries supported by yellow elastic fibers and a reticulum which forms a basement membrane covering the elastic layer supporting the epithelial layer.

The epithelium is composed of two kinds of cells,large flat plate-like cells which cover the capillaries, and between them small nucleated polygonal cells, singly or in groups in the intercapillary spaces (Dwight, 1919).

Miller (1937) says "... in normal lung, the epithelium

lining the alveolar walls is made up of thin flattened nucleated squames, which are closely applied to the alveolar wall. It is continuous epithelium."

Waters (1860) states "... that the cells of the epithelial layer form a distinct and complete coating to the walls of the air-sacs and alveoli and they rest immediately upon the basement membrane." Waters estimates the size of epithelial cells from 1/3000 to 1/5000 of an inch.

The yellow elastic tissue forms the greater part of the wall of the air-sacs and the septa between the alveoli. The fibers are arranged singly or in bundles, extending in different directions in the walls, allowing distention in all directions (Miller,1937). They also give strength and support to the walls and restore the shape of the air-sacs and alveoli in exhalation (Waters, 1860).

Some of the elastic fibers are intermingled with muscle fibers to form the myo-elastic sphincters around the mouths of the air-sacs. In the sphincters, the muscle predominates. The muscle and elastic tissue is reinforced by white collagenous fibers. Although muscle tissue is found in the edges of the larger septa that separates the air-sacs from each other, it is rare in the smaller septa. "The prevalent opinion now is that the wall of the alveolus proper contains no muscle" (Macklin, 1929). (Also, Miller, 1937).

The capillary network is supported by the elastic fibers which do not form a complete layer over the capillaries and

therefore do not interfere with the oxygenation of the blood. They form a single dense network exposed to the air of two adjacent alveoli. The capillaries are so close together that the space between them is generally smaller than the diameter of the capillaries themselves.

Diaphragm

The diaphragm is a dome-shaped transverse muscular septum that completely separates the thoracic from the peritoneal cavity. The central tendon is the highest part of the dome and all the muscle fibers are inserted in it.

The diaphragm is attached to the first three or four lumbar vertebrae, to the costal cartilages and ends of the lowest six or seven ribs, and to the posterior part of the ensiform appendix (Howells, 1901).

Mechanics of respiration

Before air can enter the lungs in inspiration the thoracic cavity must be enlarged. The radiating muscles of the diaphragm contract, causing the diaphgram to flatten. This increases the length of the chest cavity. Pressure is reduced and air from the outside goes into the lungs. The thorax is enlarged also transversely and from front to back. This is brought about mainly by the action of the intercostal muscles. The ribs are hinged at an oblique angle to the vertebral column, and this angle changes according to whether the intercostal muscles are contracted or relaxed. When contracted the muscles act on the

ribs, the angle is straightened somewhat, and the sternum is moved forward. The ribs are moved outward and upward.

During expiration, the diaphragm relaxes and moves upward, and the intercostal muscles relax so the sternum and ribs move downward and inward. During forced expiration the abdominal muscles force the abdominal viscera against the diaphragm.

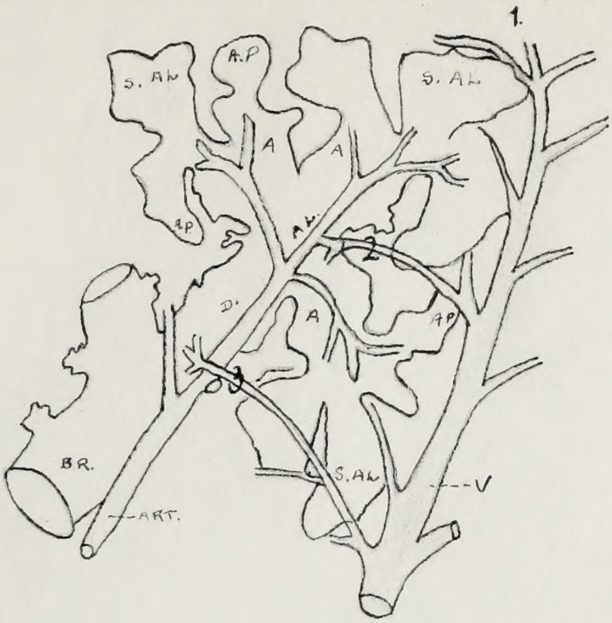


Fig. 78.—Schematic longitudinal section of a primary lobule of the human lung, showing the relation of the blood vessels to the air-spaces. BR, respiratory bronchiole; D AL, alveolar duct; A,A,A, atria; S AL, air-sacs; ART, pulmonary artery with its branches to the atria and air-sacs; V, pulmonary vein with branches from the pleura (1), from the alveolar duct (2), and from the forking of the respiratory bronchiole (3). (From Miller.)

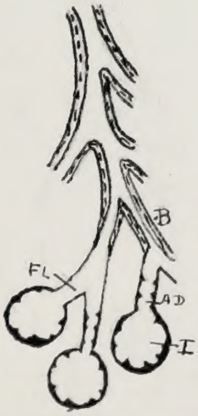


Fig. 79.—Scheme of mammalian lung structure. B,bronchus; I,Infundibulum,lined with alveoli;AD,alveolar duct; FL,bronchiole. (From Walter.)

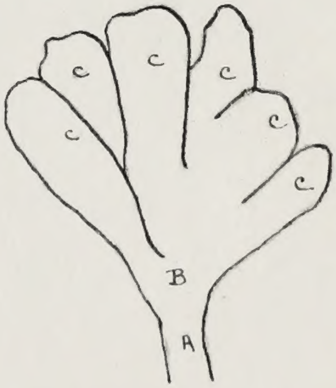


Fig.80.—Terminal bronchial tube and air-sacs in human lung. A, terminal bronchial tube; B,dilated extremity of terminal bronchial tube;C,C,individual air-sacs. (From Waters.)

SUMMARY

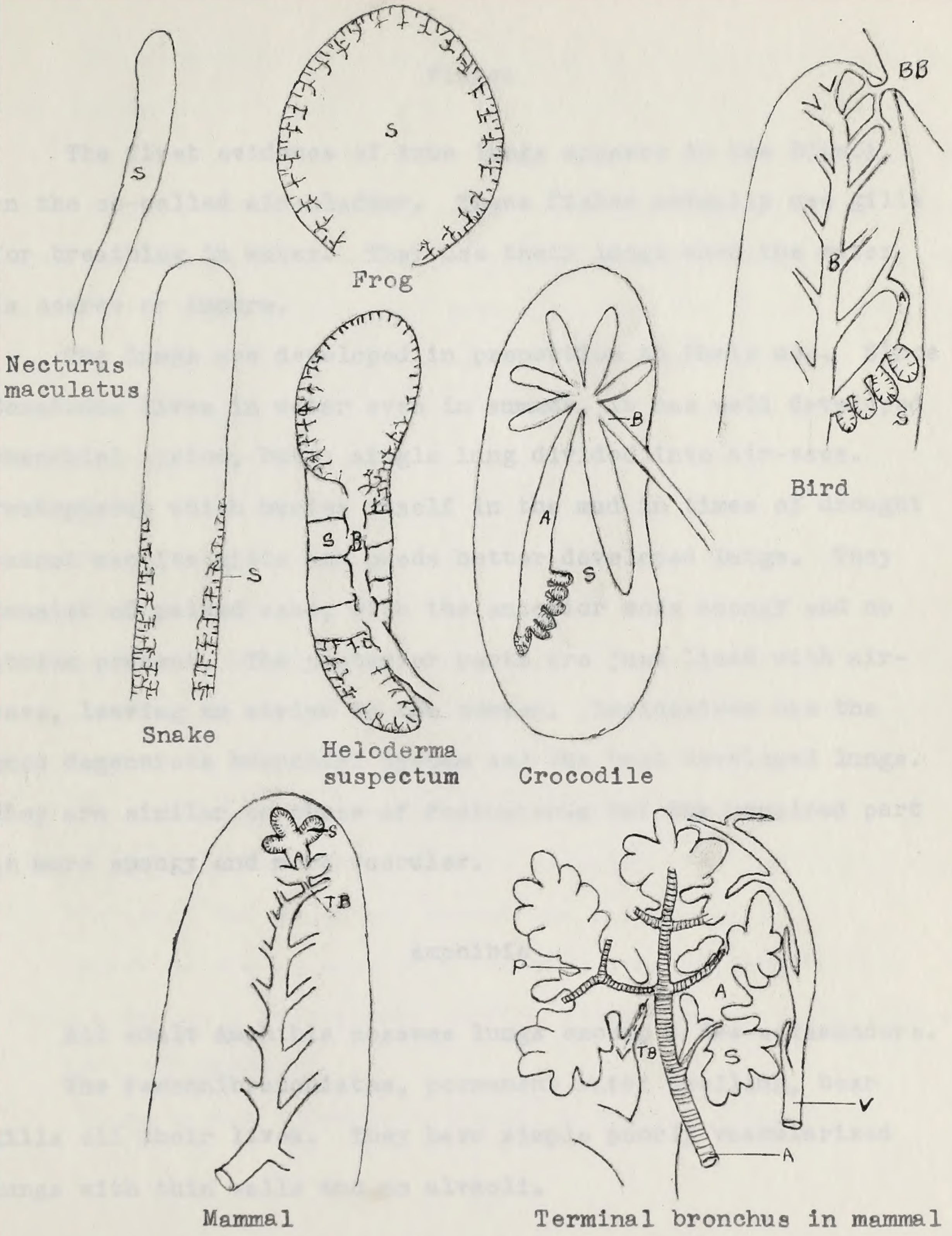


Fig. 81.—Comparison of vertebrate lungs. B,bronchus; S,air-sac A,atrium; BB, air-bag (in birds); TB,terminal bronchus;V,vestibule; P, air-sac passage; A,artery; V,vein. (From Miller.)

Pisces

The first evidence of true lungs appears in the Dipnoi, in the so-called air-bladder. These fishes normally use gills for breathing in water. They use their lungs when the water is scarce or impure.

The lungs are developed in proportion to their use. Since Ceratodus lives in water even in summer, it has well developed branchial system, but a single lung divided into air-sacs. Protopterus which buries itself in the mud in times of drought cannot use its gills and needs better developed lungs. They consist of paired sacs, with the anterior ends spongy and no atrium present. The posterior parts are just lined with air-sacs, leaving an atrium in the center. Lepidosiren has the most degenerate branchial system and the best developed lungs. They are similar to those of Protopterus but the unpaired part is more spongy and more vascular.

Amphibia

All adult Amphibia possess lungs except a few salamanders.

The Perennibranchiates, permanent water dwelling, bear gills all their lives. They have simple poorly vascularized lungs with thin walls and no alveoli.

Most Urodeles have paired lungs with smooth walls or just an indication of septa made by intersecting lines of cilia.

Among the Anura, the frog lungs show the highest degree of development. They are divided by septa into chambers that open into the atrium. The septa are highly vascular, having a double network of capillaries, each exposed to the air of one alveolus. This has the effect of doubling the respiratory surface. In toads, the chambers are shut off from the atrium by additional septa along their margins. The air-chambers are more complexly divided to meet the requirements of the more terrestrial life.

To supplement the relatively simple lung condition all Amphibia practice cutaneous respiration. The capillaries are very abundant in the skin, and carbon dioxide is transferred to the surrounding water. The oxygen is taken in mainly through the lungs.

In addition, bucco-pharyngeal respiration takes place in most Amphibians, either in the air or water. To facilitate this, the linings of the mouth and throat are very vascular.

There is one example of a tracheal lung in Typhlonectes where there is a respiratory surface along the passageway between the lung and pharynx.

Lungs have a hydrostatic function in some salamanders.

Reptilia

In addition to more highly developed lungs, Reptilia have several respiratory aids such as a nasal passage, a well developed pharynx, larynx, and trachea. It is the first group to show a real distinction between the conducting and respiratory tissue. The bronchi divide to varying degrees and in some cases approach the mammalian bronchial tree.

The bronchus in Heloderma suspectum extends to the posterior air-sac. Along its sides it is perforated by the openings of the air-sacs. In Varanus, the crocodiles, and the turtles the main bronchus has secondary and further subdivisions which lead to the air-sacs. In snakes the bronchus is a semi-cylinder.

The typical lizard lung is characterized by its simple sac-like structure, large atrium, and the honeycombed appearance of the walls of the sac. The atrium of the lung becomes smaller as the lung tissue increases. For example, in Sphenodon the lung is a simple sac and the atrium large; in Heloderma suspectum the lung tissue has increased leaving the atrium reduced to a narrow tube; in Varanus, the lung is spongy throughout with no atrium present. Varanus, in these respects, has the same characteristics as the crocodiles and the turtles. The latter has a well developed lung except for the last chamber which exhibits all degrees of complexity.

In a few lizards, finger-like projections extend from the lungs into the viscera. These are more protective than

respiratory in function as they allow the animal to puff itself up.

The snakes show more variation in their lungs. The anterior third or less is well filled with finely subdivided air-sacs. The posterior two-thirds is simple with air-cells not grouped into air-sacs. The left lung (as in some lizards) is rudimentary and may or may not be functional. Sometimes it is absent altogether. In a few snakes the two lungs are equally well developed, but the left is generally shorter. In pelagic serpents, the entire lung is spongy although less so in the posterior part. The whole respiratory surface is lined with cilia. This better developed lung in pelagic serpents is an aid to respiration and floating.

The tracheal lung is a structure found in representatives of most orders of snakes. It varies in structure, location, and connection with the lung. It may be an aid to respiration or buoyancy, but in other cases has lost its utility.

The capillary network in the septa of the alveoli is double as in Amphibia.

Although there is no diaphragm in Reptilia, the lungs in Chelonia and Crocodilia do not project freely into the body cavity but are checked by folds of the peritoneum.

Birds

The lungs are small in comparison to the size of the bird. They are very porous and spongy, light in weight, and fragile. They are very vascular and the blood is freely exposed to the air. The question of the presence or absence of epithelium lining in the alveoli is unsettled, with some authorities believing that although it hasn't yet been demonstrated it must be there.

Each bronchus continues through the lung and is called the mesobronchus. This divides into secondary and tertiary subdivisions, the latter giving off parabronchi which correspond to bronchioles in mammals.

Some bronchial tubes end in sac-like structures called air-sacs. They are permanently distended with air to some extent. Their walls are thin and non-vascular. Due to the latter fact they are not respiratory in function, but are aids in inspiration and expiration. When the bird exhales, relatively fresh air from the air-sacs return to the lungs by way of the recurrent bronchi. In inspiration, the supply of air is renewed in the air-sacs as well as in the lungs.

From the air-sacs, long narrow extensions pass into the bones and other tissues, making them pneumatic. This condition has to do with weight, flight, etc. rather than with respiration.

Birds are a link between reptiles and mammals. They have

a well developed bronchial tree, the beginning of which was evident in higher Reptilia and its ultimate development reached in Mammalia. Up to the time of a complex bronchial tree, the lung surface increased by continuous subdivision of the walls of the air-sacs into fine units. Beginning with an intricate bronchial tree, the surface is increased by more numerous and finer ramifications of the bronchial tree.

Mammalia

The characteristics of the lungs of all mammals are more or less the same, namely, a much divided bronchial tree, and lung tissue that fills the whole lung cavity leaving no atrium. The only marked difference in structure in the group appear in mammals that have adapted themselves to life in the water in contrast to the majority who live on land. The former have a more highly developed cartilagenous tissue, with rings complete dorsally, thus withstanding pressure equally on all sides. The air-sacs in aquatic forms are much larger: for example, in the manatee the largest measure about 6 mm. long by 1 to 2 mm. wide; in whales they vary from 4.71 mm. to .90 mm.; whereas in man from 5/100 to 20/100 of an inch. In water forms, the septa between the alveoli are very thick and contain a double network of capillaries, but in man the septa are thin and have a single network of capillaries. Epithelium definitely lines the alveoli in man, is probably present in the manatee, and seems to be

lacking in Cetacea. The pleura is much thicker in aquatic than in terrestrial mammals.

Diaphragm

The diaphragm plays a definite part in the mechanics of respiration only in Mammalia. In Chelonia, Crocodilia, and Aves there are certain septa sometimes referred to as diaphragms. Although these may be forerunners of true diaphragms they take no part in respiratory movements.

Ribs as an aid to breathing

The mechanics of breathing are aided by the work of the ribs and muscles. In Amphibia where ribs are absent air is swallowed in inspiration and expired mainly by the contraction of the body muscles. Ribs appear in Reptilia and are an aid to respiratory movements in all divisions of that group except turtles where they form a rigid box. In snakes, ribs are attached to the entire length of the backbone. Only the anterior ribs are used in respiration except in pelagic serpents who use the entire set. Aves, when not in flight, are aided in breathing by the work of rib muscles, but during flight these muscles are rigid. Mammalia use the ribs and intercostal muscles in increasing the width of the chest cavity.

BIBLIOGRAPHY

BIBLIOGRAPHY

Adams, Leverett Allen
An Introduction to the Vertebrates.
Wiley & Sons, 1933.
Addison, William
"On the Ultimate Distribution of the Air-passages and the Formation of the Air-cells of the Lungs."
Philosophical Transactions of Royal Society London
Vol. 132 Part 2 1842 pp. 157--163.
Anthony, H. E.
Field Book of North American Mammals
Putnam Co., 1928.
Atwood, William H.
"Visceral Anatomy of the Blacksnake."
Washington University Studies
Vol. 4 Part 1 No. 1 July, 1916 pp. 3--38.
Ballantyne, Frances M.
"Air-Bladder and Lungs: A Contribution to the Morphology of Air-Bladder of Fish."
Transactions Royal Society Edinburg
Vol. 55 Part 2 1927 pp. 371--394.
Beale, Thomas
The Natural History of the Sperm Whale.
Van Voorst (London), 1839.
Beckwith, Edwin F.
"Some Observations on the Distribution and Termination of Nerves in the Human Lung."
The Microscope
Vol. 5 1885 pp. 148--152.
Beddard, Frank E.
Structure and Classification of Birds
Longmans, Green, & Co., 1898.
-------, A Book of Whales
Putnam's Sons, 1900.
-------,"On the Trachea, Lungs, and Other Points in the Anatomy of the Hamadryad Snake (Ophiophagus bungarus)."
Proceedings Zoological Society London
Vol. 2 1903 pp. 319--328.
-------, "Contributions to the Knowledge of the Visceral Anatomy of the Pelagic Serpents Hydrus platyurus and Platyurus colubrinus."
Proc. Zool. Soc. London
Vol. 2 1904 pp. 147--154.
-------, "On the Anatomy of the Ferret-badger (Helictis personata)."
Proc. Zool. Soc. London
Vol. 2 1905 pp. 21--29.

-------, "Contributions to the Knowledge of the Vascular and Respiratory Systems in Ophidia and to the Anatomy of the Genera Boa and Corallus."
Proc. Zool. Soc. London
Vol. 2 1906 pp. 499-532.

Bishop, Sherman C.
"Notes on the mudpuppy Necturus maculosus (Rafinesque)."
Bulletin of New York State Museum, Albany
No. 268 1926 pp. 5--60.

Bostelmann, Else
"Whales, Porpoises, and Dolphins."
National Geographic
Vol. 77 Jan. 1940 pp. 35--90.

Bremer, John L.
On the Lung of the Opossum
American Journal of Anatomy
Vol. 3 1904 pp. 67--73.

Butler, Gerard W.
"On the Complete or Partial Suppression of the Left Lung in Snakes and Snake-like Lizards and Amphibians."
Proc. Zool. Soc. London
1895 pp. 691--712.

Cambridge Natural History
Vols. 7, 8, 9, 10
Macmillan & Co., 1920.

Camp, Charles L.
"Classification of the Lizards."
Bulletin of American Museum of Natural History
Vol. 48 1923 pp. 289--435.

Cantor, Theodore
"Observations upon Pelagic Serpents."
Transactions Zool. Soc. London
Vol. 2 1841 pp. 303--313.

Carte, Alexander and Macalister, Alex
"On the Anatomy of Balaenoptera rostrata."
Phil. Trans. Roy. Soc. London
Vol. 158 1868 pp. 201--261.

Coates, C. W.
"Slowly the Lungfish Gives Up Its Secrets."
Bulletin of N. Y. Zool. Soc.
Vol. 40 No. 1 1937 pp. 25--34.

Coe, W. R. and Kunkel, B. W.
"Studies on the California Limbless Lizard, Anniella."
Transactions Connecticut Academy of Arts and Sciences
Vol. 12 1906 pp. 349--403.

Cope, E. D.
"On the Lungs of Ophidia."
Proc. Amer. Philosophical Soc.
Vol. 33 1894 pp. 217--224.

Davison, Alvin
"A Contribution to the Anatomy and Phylogeny of Amphiuma means."
Journal of Morphology
Vol. 11 1895 pp. 375--410.
Dean, Bashford
Fishes, Living and Fossil
Macmillan & Co., 1895.
Dickerson, Mary C.
Frog Book
Doubleday, Doran & Co., 1931.
Droisier, W. H.
"On the Functions of the Air-Cells and the Mechanism of Respiration in Birds."
Annals and Magazine of Natural History
Vol. 17 1866 3rd series pp. 313--316.
Dwight, Thomas
Organs of Respiration in Human Anatomy
Edited by George Piersol
Lippincott Co. 7th Edition 1919.
Ecker, Alexander
Anatomy of the Frog
Translated by George Haslam
Oxford at the Clarendon Press, 1889.
Flower, William H.
"On the Anatomy of Proteles."
Proc. Zool. Soc. London
1869 pp. 474--499.
Francis, Eric T. B.
Anatomy of the Salamander
Oxford Press, 1934.
Gage, Simon Henry
"Life-history of the Vermillion-spotted Newt."
American Naturalist
Vol. 25 1891 pp. 1084--1103.
-------, Amphibia Bibliography
American Naturalist
Vol. 25 1891 pp. 1104--1110.
Gage, S. H. and S. P.
"Combined Aerial and Aquatic Respiration (in Amphibia)."
Science
Vol. 7 No. 169 1886 pp. 394--395.
Gnanamathu, C. P.
"Respiratory Mechanism of the Frog."
Journal of Experimental Zoology (Phila.)
Vol. 74 No. 2 1936 pp. 157--165.
Goodrich, Edwin Stephen
Studies on the Structure and Development of Vertebrates
Macmillan & Co., 1930.

Gunther, Albert
"Anatomy of Hatteria."
Phil. Trans. Roy. Soc. London
Vol. 157 1867 pp. 595--629.
-------, "Description of Ceratodus."
Phil. Trans. Roy. Soc. London
1871 pp. 511--571.
Haynes, F. and Laurie, Alec H.
"On the Histological Structure of Cetacean Lungs."
Discovery Reports (Cambridge Univ. Press)
Vol. 17 1937 pp. 1--6.
Headley, F. W.
"The Air-sacs and Hollow Bones of Birds."
Natural Science
Vol. 3 1893 pp. 28--30; pp. 346--352.
-------, Structure and Life of Birds
Macmillan and Co., 1895.
Hegner, Robert W.
College Zoology
Macmillan Co., 1936.
-------, Parade of the Animal Kingdom
Macmillan Co., 1940.
Holmes, Samuel J.
Biology of the Frog
Macmillan & Co., 1907.
Hopkinson, J. P. and Pancoast, S. J.
"On the Visceral Anatomy of the Python (Cuvier) described by Daudin as the Boa Reticulata."
Transactions Amer. Philosophical Soc.
Vol. 5 1837 pp. 121--134.
Howell, William Henry
An American Textbook of Physiology. Vol. 1.
2nd Edition. Saunders & Co., 1901.
Huntington, George S.
"A Critique of the Theories of Pulmonary Evolution in Mammalia."
Amer. Journ. of Anatomy
Vol. 27 1920 pp. 99--199.
Huxley, T. H.
"On the Respiratory Organs of Apteryx."
Proc. Zool. Soc. London
1882 pp. 560--569.
Irving, L.
"On the Ability of Warm-blooded Animals to Survive Without Breathing."
Scientific Monthly
Vol. 38 1934 pp. 422--428.
Jordan, David Starr
A Guide to the Study of Fishes. Vol. 1.
Henry Holt & Co., 1905.

Kellicott, William Erskine
"The Development of the Vascular and Respiratory Systems of Ceratodus."
N. Y. Academy of Sciences
Memoirs, Vol. 2 Part 4 Mar. 1905.
Kellogg, Remington
"Whales, Giants of the Sea."
National Geographic
Vol. 77 Jan. 1940 pp. 35--90.
Kerr, J. G.
"Development of Alimentary Canal in Lepidosiren and Protopterus."
Quarterly Journ. of Microscopical Science
Vol. 54 1910 pp. 483--518.
Kingsley, John Sterling
Comparative Anatomy of Vertebrates
Blakiston's Son & Co., 1912.
-------, "Systematic Position of Caecilians."
Tufts College Studies. No. 7.
Laurie, Alec H.
"Some Aspects of Respiration in Blue and Fin Whales."
Discovery Reports (Cambridge Univ. Press)
Vol. 7 1933 pp. 363--406.
Macalister, Alexander
On the Anatomy of the ostrich (Struthio camelus).
Proc. Royal Irish Academy
Vol. 9 Part 1 1865 pp. 1--24.
Macklin, Charles Clifford
"The Musculature of the Bronchi and Lungs."
Physiological Reviews
Vol. 9 1929 pp. 1--60.
Martin, H. Newell, and Moale, William A.
Vertebrate Dissection; Part 3: How to Dissect a Rodent
Macmillan & Co., 1884.
Miller, Gerrit S. and Gidley, James W.
Smithsonian Scientific Series, Vol. 9.
Published by Smithsonian Series Inc. 1938.
Miller, W. S.
"The Structure of the Lung."
Journ. of Morphology
Vol. 8 1893 pp. 165--188.
-------, "Air Spaces in Lung of Cat."
Journ. of Morphology
Vol. 24 1913 pp. 459--485.
-------, The Lung
Chas. C. Thomas Co., 1937.
Miller, W. S. and Ochsner, H. W.
"Lung of Necturus."
Bulletin Univ. Wisconsin No. 33 1900
Science Series Vol. 2 No. 3

Mitchell, S. Weir and Morehouse, George R.
"Researches on the Anatomy and Physiology of Respiration in the Chelonia."
Smithsonian Contribution
Vol. 13 1863

Müller, Bruno
"The Air-sacs of the Pigeon."
Smithsonian Miscellaneous Collections
Vol. 50 1907--1908 pp. 365--416.

Murie, James
"Researches upon the Anatomy of the Pinnipedia. Part 1. On the Walrus (Trichechus rosmarus, Linn.)."
Trans. Zool. Soc. London
Vol. 7 1872 pp. 411--464.

-------, "On the Form and Structure of the Manatee."
Trans. Zool. Soc. London
Vol. 8 1874 pp. 127--203.

-------, "On the Anatomy of the sea-lion (Otaria jubata)."
Trans. Zool. Soc. London
Vol. 8 1874 pp. 501--581.

-------, "On the Organization of the Caaing Whale (Globiocephalus melas)."
Trans. Zool. Soc. London
Vol. 8 1874 pp. 235--301.

Murie, Olaus J.
"Notes on the sea otter."
Journ. of Mammology
Vol. 21 No. 2 1940 pp. 119--131.

Newman, A. K.
"Notes on the Physiology and Anatomy of the tuatara (Sphenodon güntheri)."
Trans. and Proc. of the New Zealand Institute
Vol. 10 1877 pp. 222--239.

Newman, Horatio Hackett
Vertebrate Zoology
Macmillan & Co., 1924.

Noble, G. Kingsley
Biology of Amphibia
McGraw-Hill Book Co., 1931.

Norman, John R.
A History of Fishes
Stokes Co., 1934.

Norman, John R. and Fraser, F. C.
Giant Fishes, Whales and Dolphins
W. W. Norton & Co., 1938.

Ogawa, Chikanosuke
"The Finer Ramifications of the Human Lung."
Amer. Journ. of Anatomy
Vol. 27 1920 pp. 315--332.

-------, "Contributions to the Histology of the Respiratory
Spaces of the vertebrate Lungs."
Amer. Journ. of Anatomy
Vol. 27 1920 pp. 333--393.
Owen, Richard
"On the Anatomy of the Concave Hornbill (Buceros cavatus,
Lath)."
Trans. Zool. Soc. London
Vol. 1 1835 pp. 117--122.
-------, "Description of Lepidosiren annectans."
Trans. of Linnean Society
Vol. 18 Part 3 1839 pp. 327--361.
-------, "On the Anatomy of the Southern Apteryx (Apteryx
australis, Shaw)."
Trans. Zool. Soc. London
Vol. 2 1841 pp. 257--302.
Parker, G. H.
"The Breathing of the Florida Manatee (Trichechus
latirostris)."
Journ. of Mammology
Vol. 3 1922 pp. 127--135.
Parker, T. Jeffrey and Haswell, William A.
A Textbook of Zoology. Vol. 2.
Macmillan & Co., 1897.
Parker, William Newton
"On the Anatomy and Physiology of Protopterus annectans."
Trans. of Royal Irish Academy
Vol. 30 1892 pp. 109--226.
Parsons, F. G.
"On the Anatomy of the Petrogale Xanthopus Compared with
that of Other Kangaroos."
Proc. Zool. Soc. London
1896 pp. 683--714.
Porsild, Morten
"Scattered Observations on Narwhals."
Journ. of Mammology
Vol. 3 1922 pp. 8--13.
Racovitza, Emile G.
"A Summary of General Observations on the Spouting and
Movements of Whales."
Report of Smithsonian Institution
1902--1903 pp. 627--645.
Rainey, G.
"On the Minute Anatomy of the Lung of the Bird."
Medico-Chirurgical Society Transactions
Vol. 32 1849 pp. 47--58.
Rau, A. Subba
"Observations on Anatomy of Heart, Lungs, and Related
Parts of Ceratophyrus."
Journ. of Anatomy London
Vol. 58 Part 4 1924 pp. 306--327.

Reighard, Jacob and Jennings, H. S.
Anatomy of the Cat
2nd Edition Revised. Henry Holt & Co., 1930.
Roosevelt, James W.
"The Anatomy of the Thorax and Lungs in Relation to Certain Points in Physical Diagnosis."
Medical Record
Vol. 37 1890 pp. 201--204.
Ross, Mary J.
"Special Structural Features in Air-sacs of Birds."
Trans. Amer. Microscopical Soc.
1899 Vol. 20 pp. 29--40.
Shea, Stephen
"Observations on the Structure of the Pulmonary Alveolar Wall in the Adult Rat, Guinea Pig, and Rabbit."
Proc. Royal Irish Academy
43B 1936 pp. 73--81.
Shufeldt, R. W.
"Heloderma suspectum."
Proc. Zool. Soc. London
1890 pp. 148--244.
Sibson, Francis
"On the Mechanics of Respiration."
Phil. Trans. Roy. Soc. London
1846 pp. 501--550.
Smith, Gertrude M.
"The Detailed Anatomy of Triturus torosus."
Trans. of Royal Society of Canada
Vol. 21 Section 5 3rd series 1927.
Stirling, William
"On the Nerves of the Lungs of the Newt."
Journ. of Anatomy and Physiology
Vol. 16 1881 pp. 96--105.
Stricker, Salomon
Manual of Histology
Wood & Co., 1872.
Thompson, Joseph C.
"Contributions to the Anatomy of the Ophidia."
Proc. Zool. Soc. London
1913 (2) pp. 414--425.
Walter, Herbert E.
Biology of the Vertebrates
Macmillan & Co., 1928.
Waters, A. T. Houghton
The Anatomy of the Human Lung
Churchill Co., (London) 1860.
Watson, Morrison and Young, Alfred H.
"On the Anatomy of Hyaena crocuta (H. maculata)."
Proc. Zool. Soc. London
1879 pp. 79--107.

Watson, Morrison
"Additional Observations on the Anatomy of the spotted hyaena (Hyaena crocuta)."
Proc. Zool. Soc. London
1881 pp. 516--521.
Weysse, Arthur Wisswald
A Synoptic Textbook of Zoology
Macmillan & Co., 1911.
Whipple, Inez L.
"Ypsiloid Apparatus of Urodeles."
Biological Bulletin of Marine Biological Laboratory, Woods Hole, Mass.
1906 No. 10 pp. 255--297.
Wiedersheim, Robert E. E.
Elements of the Comparative Anatomy of Vertebrates.
2nd Edition.
Translated by W. N. Parker
Macmillan & Co., 1897.
Wilder, Burt G.
"On the Respiration of Amia."
Proc. Amer. Assoc. for Advancement of Science
Vol. 26 1876 pp. 306--313.
Williams, Thomas
"Organs of Respiration" in Cyclopaedia of Anatomy and Physiology.
Vol. 5 Supplement.
Longman, Brown, Green, Longmans, and Bros., 1859.
Willson, Herbert G.
"Terminals of Human Bronchiole."
Amer. Journ. of Anatomy
Vol. 30 1922 pp. 267--287.
Wislocki, George B.
"On the Structure of the Lungs of the Porpoise (Tursiops truncatus)."
Amer. Journ. of Anatomy
Vol. 44 1929 pp. 47--77.
-------, "The Lungs of the Manatee."
Biological Bulletin of Marine Biological Laboratory, Wood's Hole, Mass.
Vol. 68 1935 pp. 385--396.
Wislocki, George B. and Belanger, Leonard F.
"The Lungs of the Larger Cetacea Compared to Those of Smaller Species."
Biological Bulletin of Marine Biological Laboratory, Wood's Hole, Mass.
Vol. 78 No. 2 1940 pp. 289--297.
Young, Alfred and Robinson, Arthur
"On the Anatomy of Hyaena striata."
Journ. of Anatomy and Physiology
Vol. 23 (New Series, Vol. 3) 1888 pp. 90--105.

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